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NOMENCLATURE OF WATER MASSES IN THE TASMAN SEA

By D. M. Garner*

[*Manuscript received August* 6, 1958]

Summary

In a recent paper by Rochford (1957) on the identification and nomenclature of water masses in the Tasman and Coral Seas, three oceanic water masses of importance to New Zealand hydrology have been described as "Coral Sea", "Sub-Antarctic", and "East Central New Zealand". Reasons are advanced here to suggest that the origins proposed for these water masses may require modification.

I. Introduction

The paper on Tasman Sea water mass identification recently published in this Journal by Rochford (1957) makes an important contribution to the study of a little-known oceanic region. It will be particularly valuable, as the author states in his Conclusions, in guiding future work in this area.

Presently working in the field of New Zealand oceanic hydrology, which is subject to Tasman influence in major degree, the present author takes particular interest in the system of nomenclature adopted by Rochford, and some comments on the nature of three "water masses" of importance to New Zealand hydrology—the "Coral Sea", the "Sub-Antarctic" and the "East Central New Zealand"—are offered here.

II. "Coral Sea" Water

This water was defined by Rochford (1957) who used three expedition stations in the Coral Sea. *Dana* station 3665, for instance, showed the presence of a shallow (75 m) intermediate salinity maximum in the southern Coral Sea. This high salinity is regarded as typifying water characteristics originating in this area through "isolation and local evaporation of equatorial waters" (p.378). However, an intermediate salinity maximum is widespread over an extensive area of the subtropical south-west Pacific. Referring to the chart of surface salinity of the oceans compiled by Sverdrup, Johnson, and Fleming (1942, Appendix, chart IV), a Pacific maximum is found in a cell centred approximately in 20° S., 120° W. (Fig. 1). The formation here of very salty surface water will be due to an excess of evaporation over precipitation at the centre of the south Pacific subtropical anticyclone and conserved by the wind drift of surface water resulting from this pressure system. Surface water in the western part of the south tropical zone is shown in the chart cited above to be much less salty, this water being apparently derived from the northern Coral Sea region. As there is little zonal variation in surface temperature across this belt apparent in the accompanying chart published by Sverdrup, Johnson, and Fleming, westward moving surface water of high salinity will tend to sink and spread out under the lighter surface water to form an intermediate salinity maximum in the western Pacific. Continuity between these features is suggested by the results obtained from *Carnegie* stations 72 to 94 (Fleming *et al.*, 1945, pp. 213–23) worked during February and March 1929. An east-west vertical salinity section through upper water layers based on these data and extended westwards by the use of selected *Dana* stations between numbers 3587 and 3604 (November 1928) and 3665 (March 1929) (Thomsen 1937, pp. 14–18) is constructed in Figure 2. This section extends across the tropical south Pacific in latitudes 10°–15° S. between the west coast of South America and the Samoan group, thence south-westwards towards the Queensland coast of Australia. The westernmost *Dana* station links this section with Rochford's discussion. Little difficulty is experienced in combining *Carnegie* and *Dana* sections below a depth of about 100 m. The salinity maximum in the vertical water column may be traced from its highest value near the surface around 130° W. along the section and deepening towards the west, as lower salinity predominates in surface layers. The maximum salinity is progressively reduced towards the west through mixing with adjacent waters.

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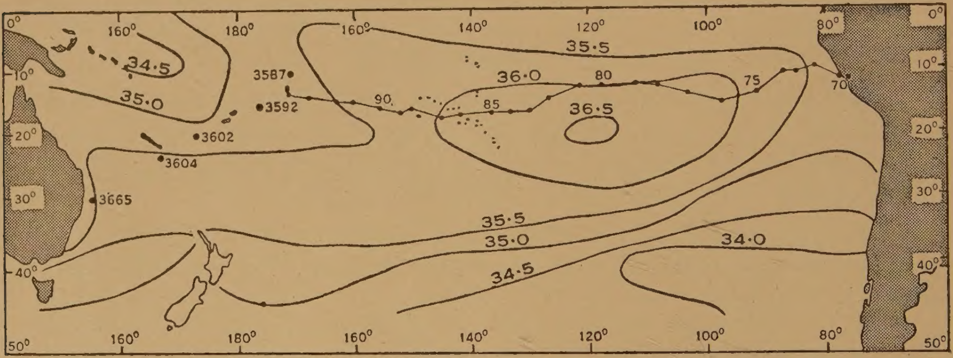

Fig. 1.—Station positions of *Carnegie* (70–94), February and March 1928, and *Dana* (3587–3665), November 1928 and March 1929. Surface salinity after Sverdrup (1942).

The possible physical continuity of water characteristics between the eastern surface source region of high salinity water and the western highly saline sub-tropical intermediate layer should be kept in mind in discussing the nature of the water labelled "Coral Sea" by Rochford.

Conclusions concerning the vertical "transfer of heat . . . without appreciable change in chlorinity" given by Rochford (1957, pp. 375 and 381) must be made with care, in that below a superficial layer exchanging heat directly with the atmosphere, mixing processes would result in a vertical eddy flux of heat *and* salt except in the trivial case of water homogeneous in one property. The Coral Sea Basin occupies a relatively small area in the extreme north-west of the Coral Sea region and can only be regarded as isolating (loc. cit., p. 376) waters below a depth of some 2700 m. The sinking of Coral Sea water along a "tropical convergence" (p. 379) to form an intermediate water is suggested by Rochford (p. 380) as a possible

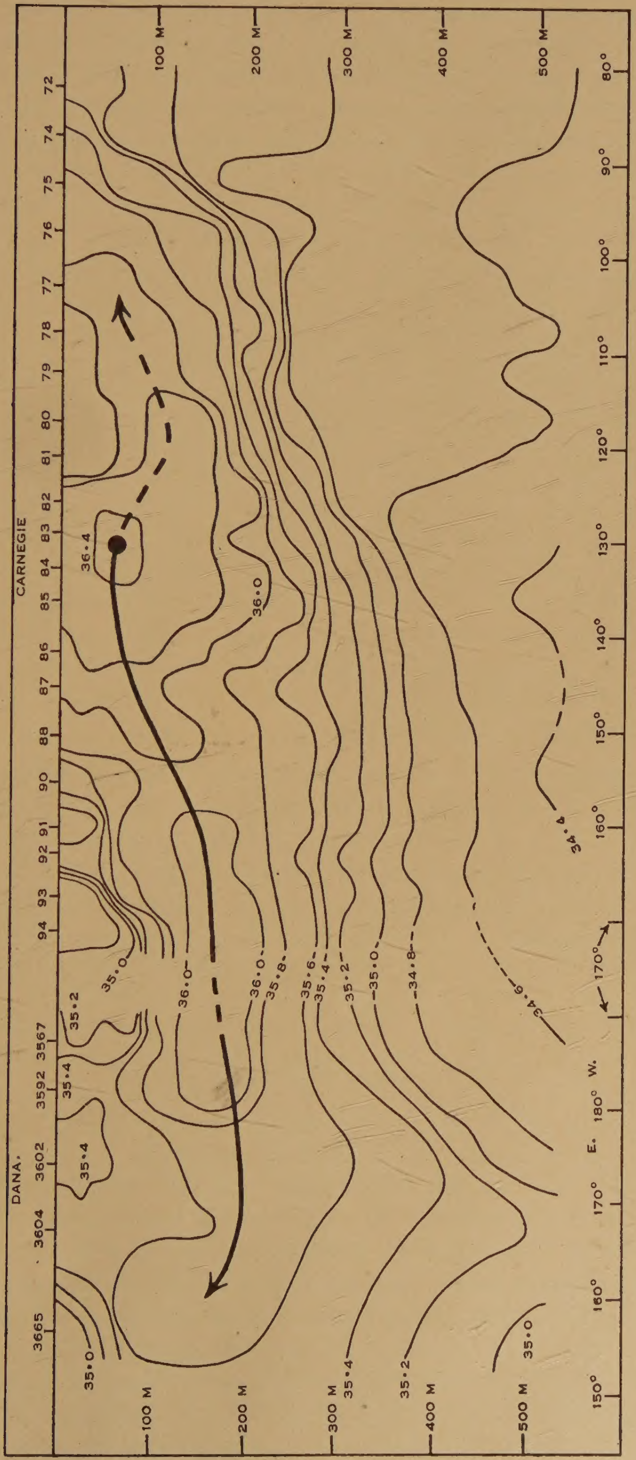

Fig. 2.—Composite cross section of salinity (‰) across the subtropical south Pacific to a depth of 500 m; constructed from *Carnegie* and *Dana* data (station positions shown in Fig. 1).

step in the process of the formation of the "Central Tasman" surface water. By entering isopleths of constant potential density in his figure 3*A* it may be seen that virtually all the water described for stations in the southern part of the meridional profile discussed is significantly heavier than the "Coral Sea" water and in the general case, the heavier southern waters would tend to sink at such a convergence.

III. "SUB-ANTARCTIC" WATER

The characteristic curve for *Dana* station 3665 is only partially presented in Rochford's figure 3*A*. At greater depths than have been plotted by Rochford, it reaches a chlorinity minimum of 19·09‰ at a temperature of 4·41°C and a depth of about 1200 m (Thomsen 1937, p. 18). This is the core of the Antarctic intermediate water formed at the surface south of the Antarctic convergence. Below this minimum, salinity increases again with the increasing admixture of Pacific deep water in the water column. The characteristics of this Antarctic intermediate water (Rochford's "deep Sub-Antarctic water" ?—p.376) are, in general, distinct from those of the Sub-Antarctic surface water which lies between the subtropical and Antarctic convergences, and retains its characteristic properties in this belt across the entire south Pacific (cf. Sverdrup, Johnson, and Fleming 1942, p. 707). The effect of the sinking of Sub-Antarctic surface water at the subtropical convergence on the salinity at intermediate depths remains to be fully evaluated in the south-west Pacific but the essential difference between this water and the Antarctic intermediate water should be kept in mind.

It would seem, then, that the geometrical construction of Rochford's figure 3*B* (loc. cit.) for deriving the composition of Tasman surface waters in terms of "Coral Sea" and "Sub-Antarctic" components (presumably through *horizontal* exchange) has been based on two points derived from the *vertical* mixing diagram of his figure 3*A*. Further, the low chlorinity point of figure 3*B* seems to represent an arbitrary point, of no special physical significance, lying between the turning points in the chlorinity distribution (partially plotted in figure 3*A*) marking the subtropical and Antarctic intermediate waters.

IV. THE SUBTROPICAL CONVERGENCE

Recent work around New Zealand has shown that the subtropical convergence can be readily recognized from the temperature distribution in surface waters east of the country. The main boundary between subtropical and Sub-Antarctic water east of New Zealand is found in coastal waters off the east coast of North Island, usually between Capes Kidnappers and Palliser. Offshore, a pronounced tongue of subtropical water is usually found carrying the subtropical convergence southwards. South-east of Banks Peninsula the convergence is usually found to turn eastwards and it may be followed to the vicinity of the Chatham Islands. While, certainly, the possession of only one water characteristic (Rochford 1957, p. 411) severely limits interpretation, the subtropical convergence has been usually readily recognizable on surface thermograph records as an abrupt change in temperature similar to that reproduced by Deacon (1945, p. 17). The limiting characteristics of subtropical water east of New Zealand seem to vary seasonally between, approximately, the temperatures 10° and 15°C, and salinities 34·6‰ to 34·8‰. The general situation described previously by the present author (in Knox 1957, fig. 22) seems to be typical. Recent work (unpublished data) has shown that relatively warm (12–14°C) and highly saline (*c.*34·9–35·0 ‰) water found off the south-west coast of South Island intrudes through Foveaux Strait in varying degrees, and has been found as far north as the South Canterbury Bight on the east coast of South Island. A sharp temperature boundary between this Tasman water, presumably of subtropical origin, and the much colder, fresher water to the south has been followed from the Otago coast, passing south of Stewart Island, and extending north-westwards into the south-east Tasman Sea. Rochford (1957, p. 408) notes that "the subtropical convergence is located further north on the east than on the west coast of New Zealand, and Sub-Antarctic waters are often found on the Chatham Rise when tropical conditions prevail in the Tasman Sea at the same latitude". This statement is not consistent with the position of the convergence west of New Zealand as sketched in figure 6 (loc. cit., pp. 384 and 385). The relatively low salinities Rochford reports in western Cook Strait may, from recent studies, be due to coastal dilution rather than the presence of the subtropical convergence to the north of this area (loc. cit., fig. 6 and p. 410).

V. "East Central New Zealand Water"

This "low chlorinity and moderate temperature water off the west coast of the North Island of New Zealand in the summer" (loc. cit., p. 408) is shown concentrated in an area (figs. 6*A* and 6*E*) under little control by the lines of sampling, Sydney towards North Cape and Sydney towards Cape Farewell. Rochford suggests that this water originates through spring and summer heating of Sub-Antarctic waters over the Chatham Rise. While the topographic "high" of the Chatham Rise seems to exert a controlling influence on water movements east of New Zealand, depths in general along the Rise are around 250–300 fm and are unlikely to account for the heating of surface waters. Whether the surface waters over the Chatham Rise are occupied by subtropical or Sub-Antarctic water (see Section IV), the predominant zonal movement seems to be eastward, the flow of Sub-Antarctic water towards Cook Strait usually being confined to a relatively narrow zone between the east coast of South Island and the subtropical tongue offshore. Current measurements have given no evidence of any large-scale mass-transport of water through the narrows of Cook Strait. The physically small dimensions of the Cook Strait narrows must also be kept in mind in considering any mass movement of water using this passage. The present author thus considers the proposed formation of the water found off the west coast of North Island, i.e. by spring and summer heating of Sub-Antarctic waters in the Chatham Rise region (loc. cit., p. 408) and its movement through Cook Strait in the early summer (p. 411) to be unlikely. There is evidence accumulating to indicate that Rochford's first suggestion of "local riverine dilution of high-chlorinity waters" (p. 408) may be a better explanation of the observed properties west of North Island.

VI. WATER "MASS" NOMENCLATURE

In geographical exploration names must be assigned to salient features to permit a description of the region. Where independent contributions are made to the exploration of a new area, the same feature may be differently labelled, leading to subsequent confusion in the literature. Also, where a name indicates the nature of its parent feature difficulty may arise when more detailed work requires some modification of the original interpretation. In oceanography both these difficulties have been felt in the study of bathymetry, and many of the principles governing nomenclature of ocean bottom features listed by Wiseman and Ovey (1953) could well be kept in mind in other branches of exploratory work.

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THE ADSORPTION OF PHOSPHATE BY ESTUARINE BOTTOM DEPOSITS

By H. R. Jitts*

[*Manuscript received November* 24, 1958]

Summary

Experiments were made on the effects of pH, phosphate concentration, particle size, iron, and organic matter on the adsorption of phosphate by estuarine bottom deposits in as natural a state as possible. Measurements of the ability of the silt to adsorb phosphate were made by isotope dilution, using ^{32}P. The silt was separated into four fractions by sedimentation.

The ability of silts to adsorb phosphate was directly related to the ratio of their contents of iron to organic matter. Organic matter depressed phosphate adsorption.

Suspensions of silts (2·99 g/1250 ml) adsorbed 80–90 per cent. of the phosphate in solutions containing 0·55 to 2·55 mg of phosphate P. This suggested that adsorption caused estuarine silts to trap phosphates during run-off periods.

I. Introduction

Investigations by this Laboratory on the nutrient cycles of estuaries (Rochford 1951; Spencer 1956), and on the artificial fertilization of oyster flats (Rochford 1951) have demonstrated the importance of the role of bottom deposits and silt loads.

The adsorption of phosphates by soils and clay minerals has been intensively studied for many years by soil scientists. Though still not conclusive, the work of such workers as Kelly and Midgley (1943) and Dean and Rubins (1947) gives strong support to the hypothesis that phosphate adsorption by soils takes place by some form of ion exchange with hydroxyl ions of the soils. The subject has been comprehensively reviewed by Wild (1950).

Apart from the work of Stephenson (1949), Rochford (1951), and Carritt and Goodgal (1954), little has been published on the behaviour of phosphates in estuarine muds. While Pearsall and Mortimer (1939) and Mortimer (1941, 1942) have made intensive studies on phosphate exchanges in lakes, it is difficult to decide how far their results can be applied to the estuarine environment.

In attempting to apply the methods and results of soil science to the study of aquatic bottom deposits, it is always necessary to keep in mind the extensive differences between them and terrestrial soils. The review on "underwater soils" by Mortimer (1949) makes this clear. In estuaries there are also the effects of changing salt concentration in the overlying water and the action of tides. The bottom deposits in estuaries are in a perpetually waterlogged condition. They are formed continuously by an electrolytic agglomeration and gravitational sedimen-

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tation of the silt load brought down by the rivers, and contain varying contributions of marine sands and organic debris. The deposits are sometimes subjected to extreme anaerobic conditions and usually support very high levels of biological activity. They invariably have an oozy or fine sandy structure containing a much higher percentage of organic matter than terrestrial soils.

In the present investigation, studies were made on the influence of pH, particle size, amount of organic matter, iron content, and phosphate concentration on the adsorption of phosphate by bottom deposits taken from sites in the Swan River, Perth, and in George's River, Sydney.

While an attempt has been made in these investigations to study the adsorption of phosphate by the muds in as natural a condition as possible, it must be pointed out that in the methods used, the muds have been thoroughly mechanically disturbed and completely aerated. Furthermore, no attempt has been made to assess the role of biological activity in phosphate fixation. The present studies relate only to the chemical mechanisms involved in the reversible adsorption of phosphate by estuarine bottom deposits in the dispersed and aerated condition.

II. METHODS

Preparation of Samples.—Samples were collected by the grab technique (Rochford 1951) from the surface of bottom muds. The samples were then thoroughly mixed and the "silt" fraction separated by washing with distilled water through a 200-mesh sieve (I.M.M. standard). The silt fraction used in all the following studies consisted of all particles of diameter less than 0·06 mm. Silt suspensions were made by diluting the silt from 20 g wet weight of whole mud to a litre (2–4 g dry weight of silt). In studies on the distribution of mineral constituents, organic matter was removed with peroxide before sieving (Piper 1944).

Fractionation of Samples.—This was done by an adaptation of the method of Piper (1944). Except where stated, salts or organic matter were not removed, nor were dispersing agents added. This was done in order to study the behaviour of the silt in a state as near to natural as possible. While this prevented a fractionation of the silt into its component minerals, it did allow reproducible fractionation into particle size ranges.

After sieving, the silt suspension was tumbled end over end in 1250 ml gas cylinders for 16 hours. Varying concentrations of labelled phosphate were then added and the suspension left standing for 24 hours with occasional vigorous stirring. This enabled the added isotope to reach a stable exchange equilibrium with the phosphate originally present in the suspension.

Immediately after a vigorous stirring, the first 20 ml pipette sample was taken as rapidly as possible from very close to the bottom. This represented an aliquot of the total suspension. Pipette samples were then taken 22 cm below the surface after time lags of 10·5 min, 43 min, and 18 hours. A portion of the remaining suspension was then centrifuged at 2500 *g* for 10 min and a pipette sample of the supernatant taken.

This method of fractionation permitted the division of the suspension into four cumulative particle size fractions containing particles with log(settling velocities) below $\bar{1}\cdot54$, $\bar{2}\cdot54$, $\bar{3}\cdot94$, and $\bar{4}\cdot54$ where the velocities are expressed in cm/sec.

These velocities would correspond to particles of diameters 0·06, 0·02, 0·01, and 0·002 mm in the International System for Mechanical Analysis (Piper 1944). However, as organic matter was not removed in many of the following experiments and many particles consisted of undispersed aggregates, the specific gravity of the particles cannot be assumed to be 2·6 as in the International System, except in the case of the upper limit of the coarsest particles that passed the sieve. For this reason the particle size fractions have been arbitrarily labelled A, B, C, and D to refer to the fractions of particles with log(settling velocities) of less than $\bar{4}\cdot54$ (fraction A), $\bar{4}\cdot54$ to $\bar{3}\cdot94$ (B), $\bar{3}\cdot94$ to $\bar{2}\cdot54$ (C), and $\bar{2}\cdot54$ to $\bar{1}\cdot54$ (D).

The 20 ml samples collected above were placed in small bottles and 5 ml of N NaOH was added to each, to bring into solution all "adsorbed phosphate" as defined by Rochford (1951). The samples were shaken vigorously and 10 ml aliquots immediately pipetted off, placed in tared nickel crucibles, and dried in an air oven at 110°C for 24 hours. This gave the dried weights of the cumulative particle size fractions, and in the case of the centrifuged sample, only the weight of salts originally present in the silt, plus the added phosphate and sodium hydroxide. This allowed calculation of the true dried weight of silt in the various fractions, and the weight of silt in each particle size range (A, B, C, and D) respectively.

The remaining 15 ml from the above sample was left standing for 24 hours and then centrifuged for 10 min at 2500 *g*. A 10 ml aliquot of the supernatant was pipetted off and its activity was measured. This permitted the calculation by isotope dilution, as described below, of the amount of phosphate adsorbed by each cumulative fraction of the silt, and thus the amount of phosphate adsorbed by each particle size range.

The dried silt was scraped from the crucibles used in the weight determination, and ground thoroughly in an agate mortar. The carbon content was then estimated.

The total iron content of the fraction was determined by estimating the iron contained in samples obtained from parallel fractionations. In these cases, no sodium hydroxide was added.

Throughout the above fractionation, pipetting of suspensions and active solutions was done with an automatic suction device as described by Piper (1944).

Estimation of Phosphate.—Sodium dihydrogen phosphate was added to the silt suspensions and the total adsorbed phosphate plus phosphate in solution was then estimated absorptiometrically by the molybdenum blue method after desorption by sodium hydroxide (Rochford 1951). "Carrier free" radioactive sodium dihydrogen phosphate was then added in suitable amounts to give an activity of approximately 10,000 counts per minute in the suspension. The weight of the tracer phosphate added was taken as negligible.

The activity of an aliquot of the unfractionated suspension was then measured after desorption with sodium hydroxide. This, divided by the chemically determined phosphate content of the suspension, gave the activity per gram of phosphate P in the suspension. The activity of an aliquot of the suspension after centrifugation and without desorption gave the concentration of phosphate in solution, and subtraction of this figure from the one above gave the amount of phosphate adsorbed by the unfractionated silt. In the same way, measurements of the activity of the fractions gave the amount of phosphate adsorbed by each fraction. Thus in each fraction the amount P_a of adsorbed phosphate P per gram of silt is

$$P_a = P_u \frac{A_f - A_s}{A_u} \times \frac{1}{W},$$

where, for a given volume of sample

P_u = amount of phosphate P, estimated chemically, in unfractionated silt;
A_u = activity of the unfractionated silt suspension;
A_f = activity of the particular silt particle size fraction;
A_s = activity of the water of suspension of the silt;
W = weight of silt in the particle size fraction.

Measurement of Radioactivity.—The equipment used for this was: (1) an Austronic SC3/100 scaling unit, with a resolving time of 20 μsec; (2) a Twentieth Century M6 skirted liquid Geiger counter, shielded with 1 in. of lead.

The technique used for liquid counting was that of Oddie (1953), but as only relative activities were required, no corrections were made for absorption of radiations. Activities used in calculations were as directly measured by the counter with corrections for decay and background only.

All measurements of activity were taken to more than 10,000 counts (probable error of less than 1 per cent.). After subtracting the background, counting rates of all samples were corrected for decay by reduction to an arbitrary time, based on a half-life of ^{32}P of 14·3 days.

Estimation of pH.—pH was determined with a Cambridge glass electrode and calomel half cell using a salt–agar bridge. The silt suspensions were stirred continuously during the determinations. Adjustment of pH was made with dilute solutions of hydrochloric acid and sodium hydroxide. It was found that the silt suspensions themselves had a high buffering capacity, and that after adjustment the pH values were maintained with variations of less than half a pH unit for periods of up to 48 hours.

Estimation of Carbon.—Organic carbon values of unfractionated silt suspensions were estimated on a macro scale by Rochford's (1951) modification of the wet combustion technique. Carbon contents of the silt particle size fractions could not be determined in this way as the samples were much too small, and were therefore determined by a semimicro dry combustion technique.* The procedure followed was to burn the sample with added bichromate in a stream of oxygen and to determine the carbon dioxide by absorption in tared ascarite. These carbon values include all organic and inorganic carbon in the sample. No corrections were made for inorganic carbon. Values thus obtained were taken only as an indication of the relative levels of organic matter contained in each fraction. Comparison of these values with those obtained by the wet combustion technique showed that organic carbon formed more than 80 per cent. of the total carbon content of the silts.

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* These estimations were carried out by the C.S.I.R.O. Microanalytical Laboratory at the University of Melbourne.

Estimation of Total Iron.—Total iron was estimated by the method described by Rochford (1951) with the following modifications: after digestion with sulphuric and perchloric acids, and the addition of distilled water, the samples were boiled for 5 min to ensure the complete redissolution of the iron salts before their absorptiometric estimation with thiocyanate.

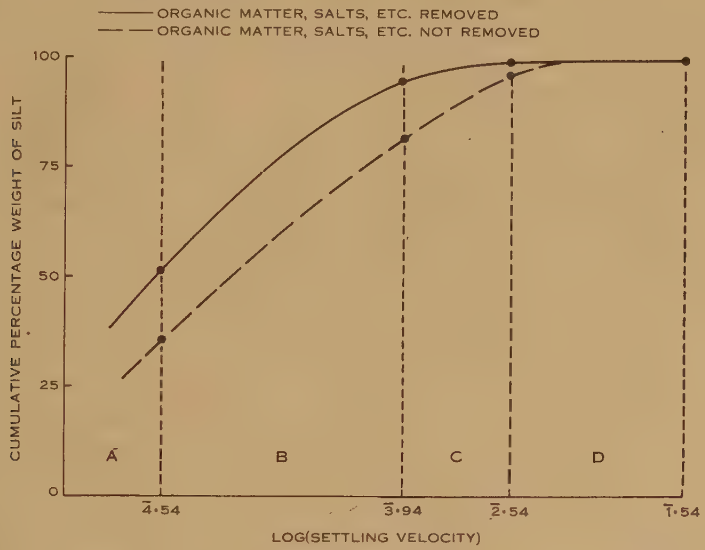

Fig. 1.—Effect of removal of organic matter, salts, etc. on particle distribution in the fractions A, B, C, and D in Crawley Bay mud.

III. Results

(*a*) *Analyses of Bottom Deposits*

"Crawley Bay mud" was taken in a depth of 6 m from a site midstream in the Swan River estuary, Perth. The Swan River is an atidal estuary which is marine-dominated in summer, and subject to isolation of the bottom waters during the winter run-off, with consequent deoxygenation, often complete, of the bottom water. During the winter run-off there is sometimes considerable silt deposition. The Crawley Bay mud is a black slimy ooze, of a highly organic nature, and contains very little marine sand.

"George's River mud I" and "George's River mud II" were taken from two adjacent intertidal flats in the George's River, Sydney. This river is a characteristic East Australian tidal estuary, marine-dominated in summer and subject to a rather regular annual variation of fresh water incursion. Its waters are thoroughly mixed vertically at all times, owing to the cellular circulation caused by tides. Muds I and II are very similar in appearance, being dark grey sandy deposits. They are both fairly organic, but contain a high proportion of marine sand and molluscan shell debris. Descriptions of the hydrological conditions in the two estuaries mentioned above have been given by Rochford (1951) and Spencer (1956).

(*b*) *Particle Size Distribution in the Silt Suspensions*

A sedimentation analysis by the method of Piper (1944) was carried out on a sample of Crawley Bay mud. The analysis was then repeated without any treatment with hydrogen peroxide, hydrochloric acid, or dispersing agent, i.e. with salts and organic matter intact.

The cumulative percentage weight distributions (Fig. 1) obtained by these two methods demonstrate that removal of organic matter and salts, and the addition of a dispersing agent, causes a breakdown of some of the larger particles into their component clay minerals. This means that the method of fractionation without removal of organic matter etc., permits the fractionation of the silt suspension into size ranges of particles in a more natural state, consisting of mineral particles cemented together with adsorbed organic matter and salts. The view that these particles are mechanically stable entities, and not merely chance debris resulting from the partial mechanical breakdown of the silt during fractionation, is supported by the fact that several fractionations of the same mud sample, using different concentrations of silt, gave very small variations in their cumulative percentage weights. An example of this is given in Table 1 for four fractionations of George's River mud I, where the maximum deviation from the mean of the cumulative percentage weights was found to be less than 3 per cent.

Table 1

PARTICLE SIZE DISTRIBUTION IN FOUR SUSPENSIONS OF GEORGE'S RIVER MUD I

Logarithms of Settling Velocities	Cumulative Percentage Weights of the Four Replicates				Mean Percentage Weight	Maximum Deviation from the Mean
	I	II	III	IV		
$\bar{1}\cdot54$	100	100	100	100	100	—
$\bar{2}\cdot54$	51·3	55·0	53·4	56·2	54·0	2·7
$\bar{3}\cdot94$	45·3	45·4	41·0	44·1	43·9	2·9
$\bar{4}\cdot54$	22·0	20·4	21·2	21·3	21·2	0·8

Comparisons of particle size fractionations of George's River mud I and George's River mud II (Table 2) demonstrate that particle size distribution in two apparently very similar muds, taken from adjacent stations having very similar hydrological environments, was very different.

(c) *Effect of pH on Phosphate Adsorption*

The silt separated with a 200-mesh sieve from 10 g wet weight of Crawley Bay mud was made up to 4 l. with distilled water. The adsorbed phosphate on the silt was removed by adding 100 ml of 2N NaOH, standing for 24 hours, and then shaking the whole for 24 hours. The suspension was then centrifuged in 100 ml tubes for 10 min at 2500 *g* and the supernatant decanted. The silt was collected, shaken with 350 ml of distilled water, recentrifuged, and once more the supernatant decanted. The silt was again collected and resuspended by shaking for 1½ hours with 4 l. of distilled water.

The effect of pH on the adsorption of phosphate by the above suspension was then studied. To 300 ml aliquots of the suspension, 3 ml of labelled phosphate solution containing 50 mg P/l. of phosphate were added. As a standard, 3 ml of the same labelled solution were added to 300 ml of distilled water. The aliquots were then adjusted by the addition of requisite quantities of dilute hydrochloric acid and sodium hydroxide to pH values of 1, 3, 5, 7, 9, and 11. After shaking for 24 hours with periodic adjustments of the pH, aliquots of the samples were centrifuged for 10 min at 2500 *g* and the activities of the supernatants measured. From these, the percentage of the added phosphate adsorbed by the silt at the respective pH values was calculated.

TABLE 2

COMPARISON OF PARTICLE SIZE DISTRIBUTION IN FOUR FRACTIONS IN GEORGE'S RIVER MUDS I AND II

Fraction	Logarithms of Settling Velocities	Weight Distribution (%)	
		George's River Mud I	George's River Mud II
A	$<\bar{4}{\cdot}54$	21	38
B	$\bar{4}{\cdot}54$ to $\bar{3}{\cdot}94$	24	33
C	$\bar{3}{\cdot}94$ to $\bar{2}{\cdot}54$	9	9
D	$\bar{2}{\cdot}54$ to $\bar{1}{\cdot}54$	46	20

Figure 2 shows that almost complete phosphate adsorption took place between pH 3 and 7, with only slight adsorption at pH values 1 and 11.

(d) *Effect of Removal of Organic Matter and Salts on Phosphate Adsorption*

Two samples of Crawley Bay mud were subjected to a sedimentation fractionation. Prior to the fractionation, the first sample was freed from organic matter and salts, and then 1 mg P (in the form of sodium dihydrogen phosphate) was added, plus sufficient radioactive phosphate to give 10,000 counts per minute. The adsorbed phosphate, organic matter, etc., of the second sample were not removed, and to it was added only the radioactive phosphate.

The adsorbed phosphate in the fractions from the two samples was estimated and the results are shown in Figure 3. In the sample from which organic matter and salts had been removed, the ability of the fractions to adsorb phosphate showed an inverse relationship with particle size, suggesting that surface area and the ability to adsorb phosphate were related. In the sample which had not been treated with peroxide and hydrochloric acid, no such relationship appeared. This is possibly due to the greater specific area of the larger particles, formed as they were from several smaller particles cemented together.

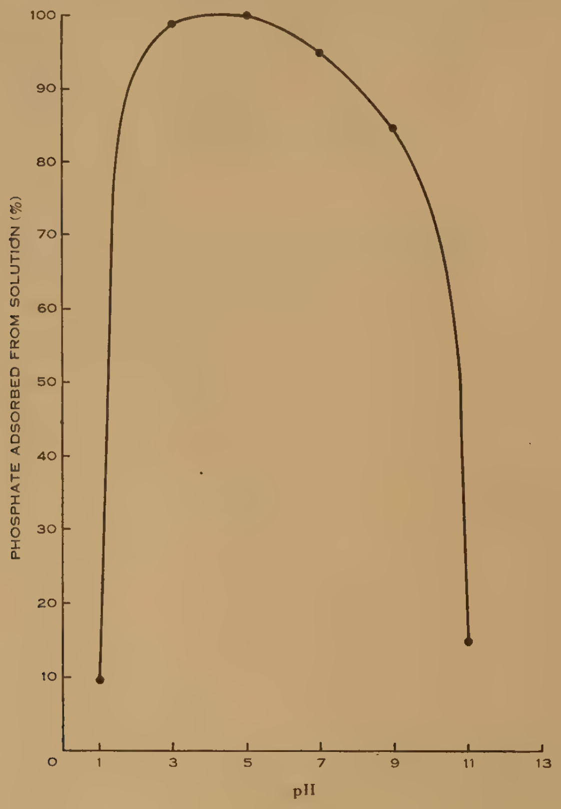

Fig. 2.—Effect of pH on phosphate adsorption by Crawley Bay mud.

(e) *Effect of Phosphate Concentration on Adsorption*

Four uniform suspensions of George's River mud I were made, and equal amounts of radioactive phosphate were added to each. Each suspension contained 0·55 mg of phosphate P and 3·79 g of silt in a total volume of 1250 ml. To the first nothing else was added, but to the second, third, and fourth, sodium dihydrogen phosphate was added giving concentrations of 1·05, 1·55, and 2·55 mg phosphate P per 1250 ml of suspension respectively.

The four suspensions were then fractionated and the adsorbed phosphate estimated for each of the four particle size ranges A, B, C, and D.

Figure 4 shows that the four fractions had greatly varying abilities to adsorb phosphate, and that this ability was not directly related to the particle size. It was also found that fraction C was capable of adsorbing up to 3 mg phosphate P per 1 g of silt.

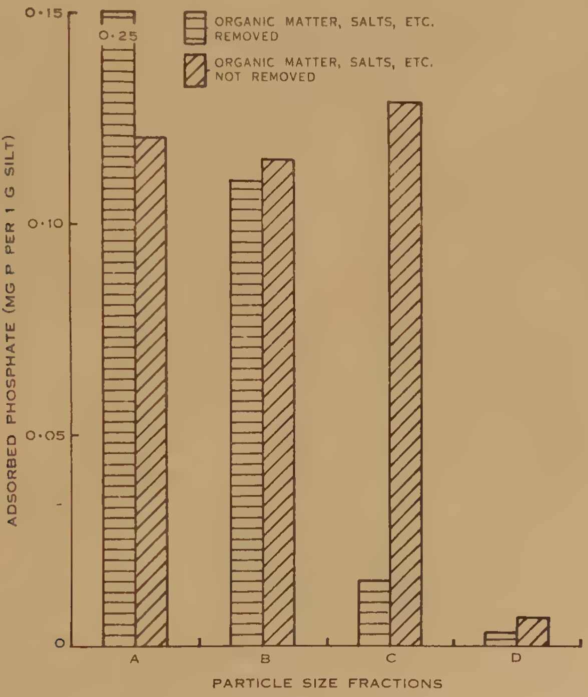

Fig. 3.—Effect of removal of organic matter, salts, etc. on phosphate adsorption by Crawley Bay mud.

This experiment was then repeated with four uniform suspensions of George's River mud II, containing 2·99 g of silt with 0·39 mg phosphate P per 1250 ml of suspension. Again radioactive phosphate and, in the case of the second, third, and fourth suspensions, 0·5, 1·0, and 2·0 mg P (in the form of sodium dihydrogen phosphate) were added. The four suspensions were fractionated and the adsorbed phosphate of the fractions estimated. The results are shown in Figure 5. Whilst the four fractions showed similar variations to those of George's River mud I, these variations were not nearly as great. A comparison of the adsorption characteristics of the two muds is shown in Figure 7(*c*).

George's River mud II was shown to adsorb only up to 1 mg phosphate P per 1 g of silt in fraction C. Figure 6 shows the variation in percentage phosphate adsorbed by 2·99 g of silt with increasing phosphate concentration in the suspension.

(*f*) *Distribution of Iron and Carbon in the Particle Size Fractions*

Duplicate suspensions of George's River muds I and II, identical with those used in the above experiments, were fractionated and analysed for total iron and for carbon. The results are shown in Figure 7.

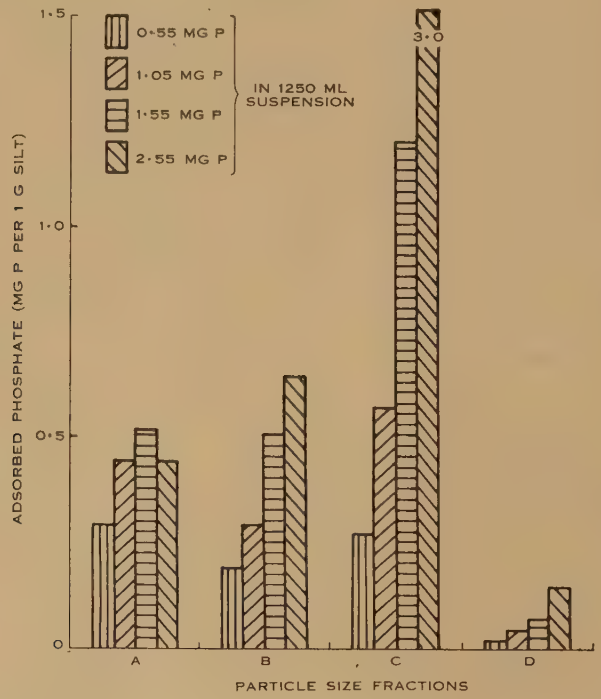

Fig. 4.—Effect of concentration on phosphate adsorption by George's River mud I.

The carbon distribution in the two muds was found to be very similar, carbon content increasing with diminishing particle size. However, the iron distribution in the two muds showed considerable differences. In George's River mud I, fraction D contained only 2·4 mg of Fe per 1 g of silt, whilst the fraction C contained a maximum of Fe at 39·1 mg of Fe per 1 g. George's River mud II contained 9·3 mg of Fe per 1 g of silt fraction D, and thereafter the iron content rose with diminishing particle size, giving no peak in fraction C as did the first mud.

IV. Discussion

(*a*) *Mechanism of Phosphate Adsorption*

The curve obtained for the effect of pH on phosphate adsorption by estuarine silts (Fig. 2) was compared with those of Kelly and Midgley (1943) for various soils and minerals, and those of Carritt and Goodgal (1954) for a river sediment and two minerals. This showed that there is at least good prima facie evidence that the chemical mechanism of phosphate bonding in estuarine silts is similar to that in soils and clay minerals.

There is very strong evidence (Wild 1950) that iron is intimately involved in phosphate adsorption by soils, though the exact mechanism is not clear. It is not even certain whether it is the iron in clay minerals or free hydrous oxides that plays the dominant role. It is for this reason that in the present studies total iron content of the silt fractions was estimated. However, no consistent direct correlation was found between the iron content and the ability of the silt to adsorb phosphate.

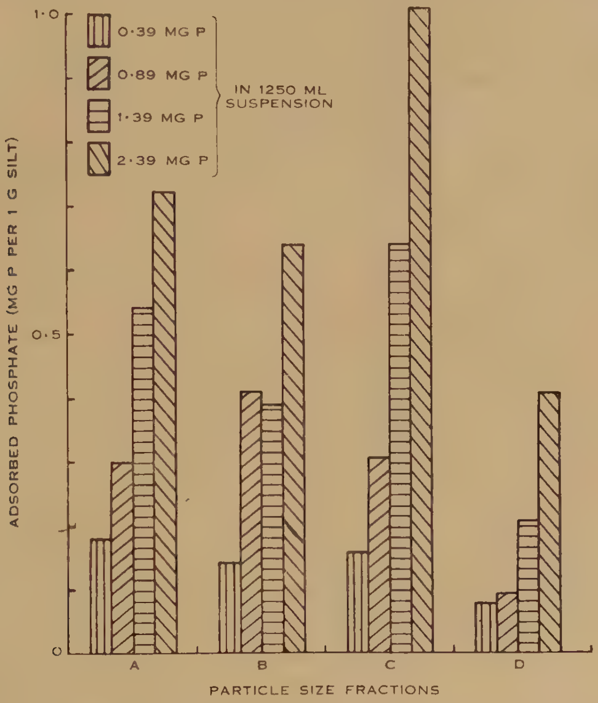

Fig. 5.—Effect of concentration on phosphate adsorption by George's River mud II.

These results made it evident that in estuarine silts some other factors were playing an unusually dominant role in phosphate adsorption by the silt. The most obvious difference between the composition of estuarine silt and average soils is the very high concentration of organic matter in estuarine silts. Wild (1950) refers briefly to the suggestion that in soils, organic matter has a depressant effect on phosphate adsorption. With this in mind, an effort was made to determine the effect of organic matter concentration in the silts studied.

A correlation was sought between the phosphate adsorbing capacity of the silt fractions and the ratio of their iron to organic matter content. This was done

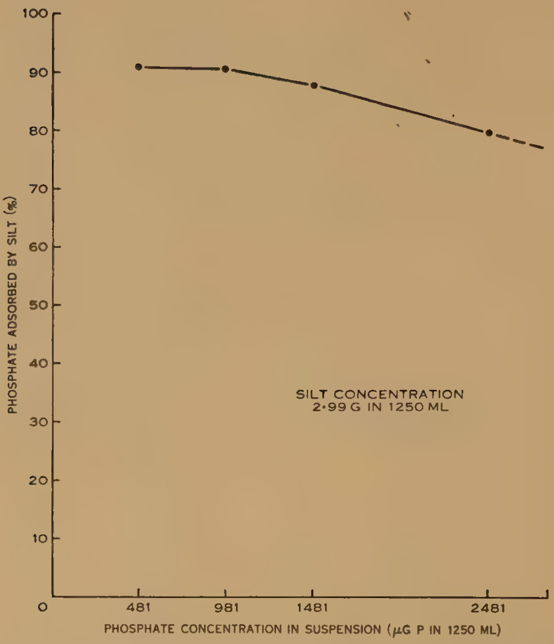

Fig. 6.—Percentage phosphate adsorption by unfractionated George's River mud II.

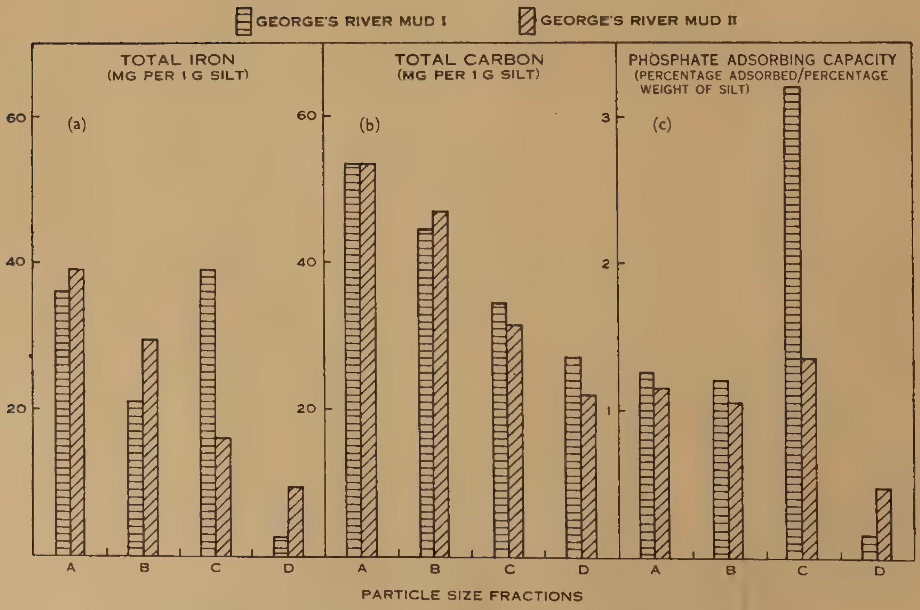

Fig. 7.—Comparison of George's River muds I and II.

for the two silts, George's River mud I and mud II, by plotting the phosphate adsorbing capacities of the fractions (as shown in Fig. 7(*c*)) against the ratio of their percentage iron to percentage carbon content. The relationship, shown in Figure 8, proved to be remarkably good. From these results it can be deduced that in estuarine silts, phosphate is adsorbed by a mechanism similar to that found in soils, in which iron is directly involved. The high organic matter content of the silt, however, has a depressant effect on phosphate adsorption.

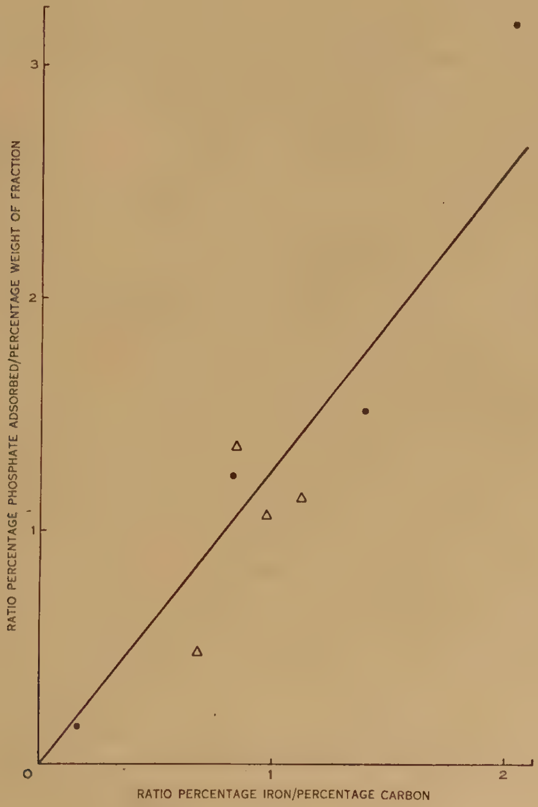

Fig. 8.—Relation between phosphate adsorbing capacity and iron/carbon ratio in George's River mud: ●, mud I; △, mud II.

While these experiments have shown that total iron and organic matter concentrations can give useful indications of the phosphate adsorbing abilities of silt, these indications must be regarded only as approximate and relative. Much more work must be done on the forms and behaviour of the iron. Baas Becking (1956) has shown that the iron in estuarine silts enters into complex and variable combinations. Moreover it is probable that aluminium can perform a function similar to that of iron in phosphate adsorption (Wild 1950).

(b) *Role of Organic Matter*

The results of these studies show that organic matter in silts plays at least two important roles in the adsorption of phosphates. Firstly, they show that organic matter can have a very marked influence on the effective sizes of the silt particles. It was suggested in Section III that this was due to the cementing of several smaller particles into larger composite ones by organic matter. This has been confirmed by some microscopic examinations of George's River silts by Baas Becking (unpublished data) using a pectin stain on silt particles that had been dried and carefully fractionated by conventional sieve methods. It was shown that many of the larger particles were in fact composed of several smaller particles very firmly cemented together in a sheath of organic matter.

The second and perhaps more important role of organic matter is its considerable depressant effect on phosphate adsorption. Whether this is due to a competitive combination with the active phosphate-adsorbing elements of the silt or merely a physical masking of the silt particles from the phosphate ions in solution is not made clear in these experiments. Whilst it is probably a combination of the two possibilities, the masking effect is the more likely.

(c) *Significance of Adsorbed Phosphate*

The studies on the effect of phosphate concentration on adsorption have shown that silts are capable of adsorbing very large quantities of phosphate, and that in the natural state they seldom even approach saturation with phosphate. It follows then that under average conditions the silt would act continuously as a trap of phosphate at the expense of the overlying water, particularly during the freshwater run-off cycle when highly oxygenated waters with low salinity are bringing down large quantities of terrestrial phosphate and silt. The reverse desorption of the phosphate into the overlying water can take place only under very extreme conditions of oxygen depletion and possibly under the action of hydrogen sulphide sometimes produced by biological activity (Baas Becking and Mackay 1956). Diffusion of phosphate into phosphate-poor waters would be both slow and only small in quantity.

Carritt and Goodgal (1954) have demonstrated that phosphate is adsorbed by silt in two stages, the first rapid and reversible and the second much slower and reversed only with difficulty. Their first stage is apparently identical with the phosphate adsorption investigated in the present studies, but the nature of the second stage is not clear. Possibly it is a combination of both biological fixation of the phosphate and a gradual physical penetration of phosphate ions into the lattices of the mineral constituents of the silt.

In estuarine silts, adsorption of phosphate from the overlying waters, either during deposition or later, supplies phosphates to the estuarine benthos. The relationship of adsorbed phosphate to the overlying water is probably largely indirect, e.g. through exudation of phosphates by plants, and also its release by decay of organic matter. The fate of the adsorbed phosphate that penetrates the mineral lattices is not known, but as it is irreversibly fixed, it may be lost to the general phosphate economy of the estuary.

It has been shown that during the freshwater run-off periods, when biological activity is usually low, estuarine silts can trap a large part of the high concentrations of phosphate in the waters. This phosphate is then available for gradual biological utilization when conditions are more suitable and also for eventual release into the overlying water of the estuary during the more stable periods. This could increase the amount of phosphate available, and thus play an important part in the high level of productivity characteristic of estuaries.

V. Acknowledgments

Thanks are due to the Institute of Agriculture and the Department of Chemistry of the University of Western Australia for facilities and assistance.

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THE POPULATIONS OF AUSTRALIAN "SALMON", *ARRIPIS TRUTTA* (BLOCH & SCHNEIDER), IN AUSTRALIAN WATERS*

By W. B. Malcolm†

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Summary

In Australian waters the stock of Australian "salmon", a percomorph form, is composed of two clearly defined populations. These populations are referred to as the eastern and western subspecies. The western subspecies is normally the only group found in Western and South Australia, whereas the eastern subspecies is normally the only group found in New South Wales. The distributions of the subspecies overlap in Tasmania and Victoria.

The subspecies differ in the number of rakers on the first gill arch; the western subspecies has 25–31 rakers, the eastern subspecies 33–40. The number of gill rakers can be related to the mode of feeding as the predominant food of the western subspecies is the pilchard, *Sardinops neopilchardus* (Steindachner), while that of the eastern subspecies is the euphausiid, *Nyctiphanes australis* Sars.

Small but significant differences are evident in the number of rays in the dorsal fin, and in the number of scales around the girth.

I. Introduction

In a preliminary account of the investigations on the Australian salmon, a percomorph species, Fairbridge (1950) reported the presence of several races. The taxonomic status of these was by no means clear, but Fairbridge suggested that separate breeding populations were present in both New Zealand and Lord Howe Island waters, and that two or possibly three separate breeding populations were present along the Australian coast.

Fairbridge presented morphological and other evidence to show that the Australian stock is certainly divisible into two populations. The distribution of these populations, designated by Fairbridge as subspecies, is shown in Figure 1. The western subspecies is normally the only group found in Western and South Australia, whereas the eastern subspecies is normally the only group taken in New South Wales. The distributions of the subspecies overlap in Tasmania and Victoria. The presence of a third breeding population in Australian waters was postulated by Fairbridge; this postulate requires the subdivision of the western subspecies into two separate breeding populations.

As Fairbridge had not completed the racial study by the time of his death, a complete revision of the morphological examination initiated by him has been undertaken. This revision, however, has been confined to the salmon frequenting the onshore waters of Australia; the investigations were not designed to further the existing knowledge of either the Lord Howe Island or New Zealand populations.

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* Part of a thesis submitted for the degree of Doctor of Philosophy of the University of Western Australia.

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A preliminary racial analysis, using a large number of conventional features, was carried out on material from all main localities throughout the Australian distribution to determine suitable morphological features for typifying the populations. The selected features comprised the number of rakers on the first gill arch, the number of rays in the dorsal fin, and the number of scales around the girth. These features were also used by Fairbridge.

Throughout the text, the term "population" is used in a general sense to denote a breeding community which may be of racial, subspecific, or specific status.

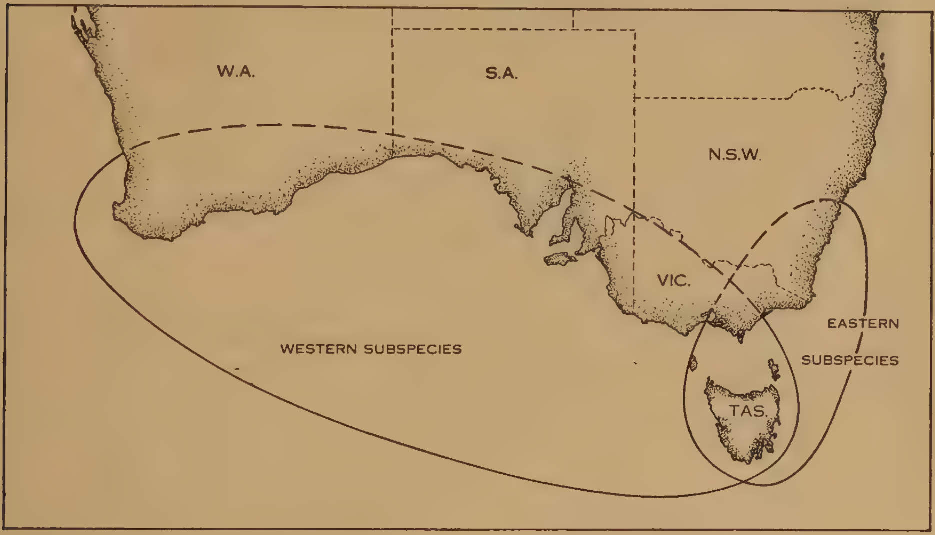

Fig. 1.—General distribution of the eastern and western subspecies.

II. Gill Rakers and Population Differentiation

Gill raker material was collected from all possible localities throughout the distribution but, for convenience, the data have been grouped for the following main areas: New South Wales, Tasmania–Victoria, South Australia, and Western Australia.

The gill raker count has been confined to the rakers on the first gill arch; no subdivision into upper and lower arms has been made. Initially, both left and right sides were considered but, as no significant difference existed between the means of the counts of the two sides, the left side has been used for the majority of specimens, and only the data pertaining to the left side are considered. In the adult specimens no difficulty was experienced in counting the rakers with the naked eye, but the gill arches from juvenile specimens were examined under a binocular microscope to detect and count the vestigial rakers.

The counts are in agreement with those of Fairbridge (1950) and are presented graphically in Figure 2. The total range of gill rakers encountered was 25–40, but two well-defined modal groups are present. A low raker group comprises fish with 25–31 rakers while a high raker group comprises fish with 33–40 rakers. Although approximately 4000 gill arches have been examined, no overlapping of the two modal groups has been detected. Western Australian and South Australian fish are of the low raker group, New South Wales fish are of the high raker group, while in Tasmania and Victoria both groups are encountered and are, in fact, present in the same schools. It is thus possible to divide the stock of salmon in Australian waters into two populations which are geographically isolated over the greater part of their range. The populations probably represent true biological species (Malcolm, unpublished data), but until direct evidence of their reproductive isolation is obtained, it is best to consider them as subspecies. The low raker group is referred to as the western subspecies, the high raker group as the eastern subspecies (Fig. 1).

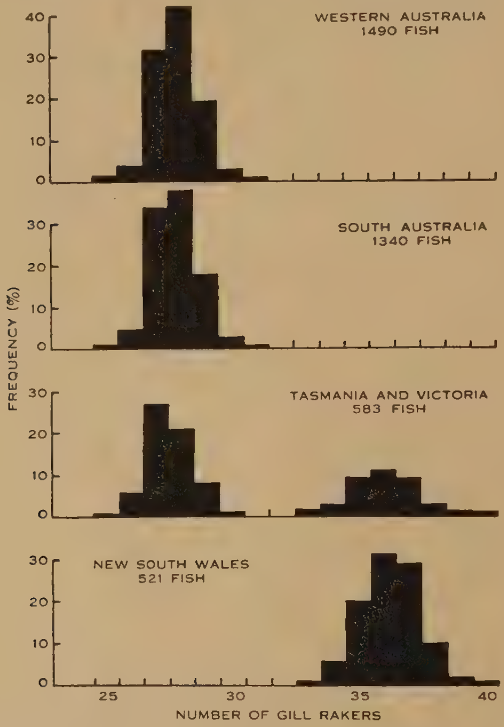

Fig. 2.—Gill raker counts from the main areas in southern Australia.

Although in most areas in Tasmania and Victoria the schools of Australian salmon contain both eastern and western subspecies, one or the other form, dependent on the area, normally predominates. In western Victoria the schools are composed of western subspecies fish or else the western subspecies predominates when mixing occurs. The eastern subspecies is the predominant form in eastern Victoria. In Tasmania the north-eastern areas are predominantly occupied by the eastern subspecies while the western subspecies is the dominant form elsewhere.

III. DORSAL FIN

As the number of spines in the dorsal fin was constant in almost all specimens examined, the dorsal fin count was confined to the soft rays. The counts were undertaken on fresh fish whenever possible as some difficulty was normally encountered in the elevation of the fins and the separation of the rays in preserved material. When the last two rays were paired they were separated and counted individually.

The fin ray data are presented in Table 1; these data have been divided into eastern and western subspecies (on the basis of the number of gill rakers), and have been grouped by each of the major distribution areas. For the western subspecies, Western Australian, South Australian, and Tasmanian–Victorian samples show the same range of 15 to 19 soft rays and have similar mean values; the maximun difference between a major area sample mean and the mean of the western subspecies combined data is 0·05 fin rays. Samples of the eastern subspecies from New South Wales and Tasmania–Victoria show the same range of 15–18 soft rays and have identical means. The western subspecies combined data mean and the individual sample means differ from those of the eastern subspecies by approximately one fin ray.

TABLE 1

DORSAL FIN COUNT DATA

Locality	No. of Fish having Fin Ray Counts of					No. of Fish	Arithmetic Mean	Standard Deviation of the Mean	Standard Error of the Mean
	15	16	17	18	19				
Western Subspecies									
Western Australia	4	58	162	79	4	307	17·07	0·740	0·042
South Australia	5	44	202	98	6	355	17·16	0·707	0·038
Tasmania–Victoria	1	37	134	57	3	232	17·10	0·682	0·045
Combined Data	10	139	498	234	13	894	17·11	0·713	0·024
Eastern Subspecies									
Tasmania–Victoria	14	74	27	2		117	16·14	0·633	0·059
New South Wales	23	128	43	4		198	16·14	0·629	0·045
Combined Data	37	202	70	6		315	16·14	0·630	0·035

The data presented in Table 1 have been converted into graphical form (Fig. 3) for the detection of the significance of differences between the means by the method of Hubbs and Hubbs (1953). The significance of the difference between any two means is appraised by comparing the relative length and the overlap or separation of the bars denoting $2\sigma_M$ on either side of the mean.* These bars are the rectangles of Hubbs and Perlmutter (1942) who determined "that considerable reliance can be placed on the significance of the difference between samples, if the corresponding rectangles are only slightly separated, or if the overlap is not more than about 33 per cent. of the length of the shorter of the two rectangles". From Figure 3 it is apparent that for the western subspecies the differences between the means of the Western Australian, South Australian, and Tasmanian–Victorian samples are not significant. Similarly, for the eastern subspecies, there is no statistical significance between differences in the New South Wales and Tasmanian–Victorian data. However, as the bars denoting $2\sigma_M$ on either side of the mean of the western subspecies samples are widely separated from those of the eastern subspecies

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* σ_M = standard error of the mean.

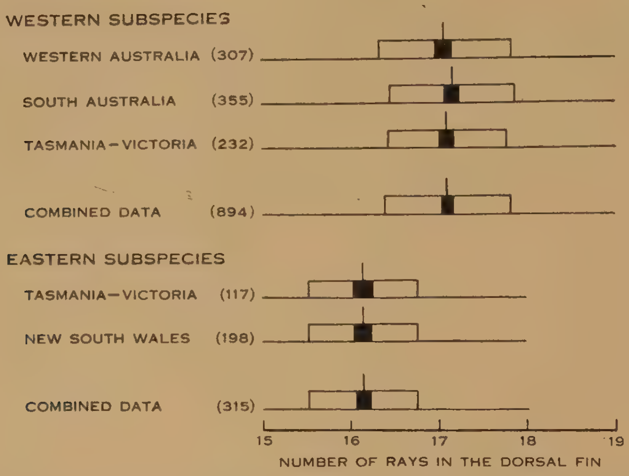

Fig. 3.—Summary of data on dorsal fin counts. The horizontal line for each sample indicates the range, the vertical line the arithmetic mean. On either side of the vertical line, the total bar represents one standard deviation of the mean while the darkened portion represents two standard errors of the mean ($2\sigma_M$). The number of fish in each sample is shown in brackets.

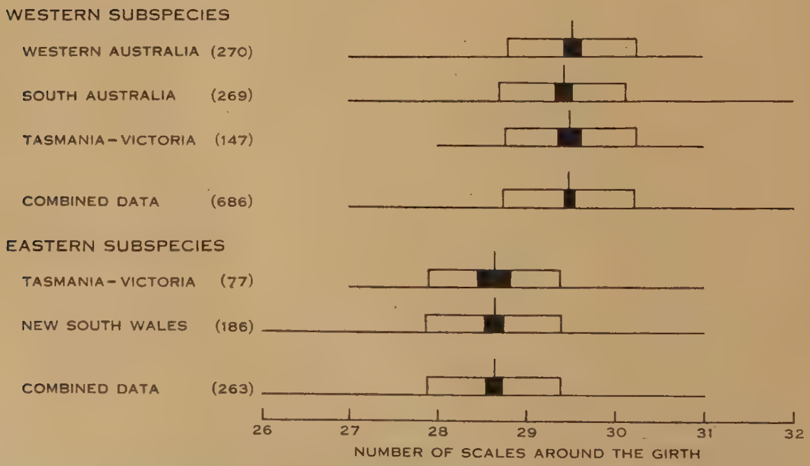

Fig. 4.—Summary of data on girth scale counts. For explanation see Figure 3.

samples, it is evident that the differences between the means of the eastern and western subspecies are highly significant when the combined data or the individual samples are compared.

When the *t* test was applied to the combined eastern subspecies and the combined western subspecies data, a *t* value of 22·8, denoting a high level of significance in the difference between the means, was obtained.

IV. Girth Scales

This count was carried out from both sides of the fish from, but not including, the eleventh lateral line scale diagonally downwards until the two lines met in the mid-ventral area. Because of some asymmetry in the scalation of most specimens, the lines from either side did not necessarily meet in the mid-ventral line. The count provided little difficulty although some specimens were discarded because of confused scalation in the mid-ventral area.

Table 2

GIRTH SCALE COUNT DATA

Locality	No. of Fish having Girth Scale Counts of							No. of Fish	Arithmetic Mean	Standard Deviation of the Mean	Standard Error of the Mean
	26	27	28	29	30	31	32				
Western Subspecies											
Western Australia		1	14	117	117	21		270	29·53	0·730	0·044
South Australia		2	12	144	95	15	1	269	29·42	0·716	0·044
Tasmania–Victoria			9	67	59	12		147	29·50	0·736	0·061
Combined Data		3	35	328	271	48	1	686	29·48	0·726	0·028
Eastern Subspecies											
Tasmania–Victoria		2	33	34	7	1		77	28·64	0·742	0·085
New South Wales	1	10	66	91	17	1		186	28·62	0·770	0·057
Combined Data	1	12	99	125	24	2		263	28·63	0·761	0·047

The girth scale data have been treated in a similar manner to the dorsal fin data; the data have been divided into eastern and western subspecies, on the basis of the gill raker number, and then grouped for each of the major distribution areas (Table 2).

The pattern shown by the girth scale data is identical with that shown by the dorsal fin. For the western subspecies, the mean values of the Western Australian, South Australian, and Tasmanian–Victorian samples are similar; the greatest variation of any of the sample means from the mean value of the western subspecies combined data is 0·06 scales. For the eastern subspecies, the Tasmanian–Victorian and New South Wales sample means are almost identical; the means of these samples vary from the eastern subspecies combined data mean by only 0·01 scales. However, the western subspecies combined data mean and the individual western subspecies sample means differ from those of the eastern subspecies by almost one scale.

When the girth scale data are converted to graphical form (Fig. 4), it is evident that the differences between the means of the eastern and the western subspecies girth scale counts are highly significant when either the combined data or the individual area samples are compared. However, there is no significance in the differences between the means of the individual area samples within each subspecies.

The application of the *t* test to the combined eastern subspecies data and the combined western subspecies data yielded a value of 15·9; this value denotes a high level of significance in the difference between the means.

V. DISCUSSION

No sex variation has been detected for the gill rakers, and although it has been shown that in some species the number of rakers varies with size (McHugh 1951; Howard 1954; Andreu 1955), the distinct modal groups demonstrated for the Australian salmon cannot be attributed to such variation. In both juveniles and adults the two groups are clearly differentiated.

It has been shown (Schmidt 1921; Taning 1952) that variation in the meristic features may be produced by the environmental conditions experienced by the fish in its early life history. McHugh (1951) has attributed gill raker variation in the anchovy *Engraulis mordax mordax* Girard to latitudinal variation in temperature. Changes in the rate of development have been shown to produce meristic variation, and it may well be that the environment influences the meristic features by increasing or decreasing the rate of development of the fish during its early life history (Hubbs 1926, 1927, 1941).

Evidence has been obtained to show (Malcolm, unpublished data) that the spawning area of the eastern subspecies is geographically isolated from that of the western subspecies, and that in relation to its overall distribution, each subspecies spawns in a very limited area. However, as the entire life history of each of the subspecies is completed in the same narrow latitudinal band, it is unlikely that the environmental conditions experienced by the subspecies could differ by such magnitude as to be responsible for the marked difference in gill raker number. There is considerable difference in the growth rate of the subspecies (Fairbridge 1950; Malcolm, unpublished data) and it is probable that the rate of development of the various meristic features will also differ. However, it is not conceivable that a difference in rate of development can be responsible for the two clearly defined gill raker groups.

The subspecies have different feeding habits, and the number of rakers on the gill arch is undoubtedly related to the mode of feeding. The eastern subspecies is a plankton feeder and exists almost entirely on the euphausiid, *Nyctiphanes australis* Sars; in addition to having the higher number, this subspecies has long and comparatively fine rakers. The western subspecies has as its main diet the pilchard, *Sardinops neopilchardus* (Steindachner), and has short and stubby rakers in addition to the reduced number.

As the subspecies spawn in different areas, it is possible that the early juveniles experience different environmental conditions. Although it is considered that these conditions would not be sufficiently different to produce the difference in the number of gill rakers, they may account for the small but significant difference in the number of rays in the dorsal fin and the number of scales around the girth. However, as the subspecies have different growth rates, possibly of dietary rather than environmental origin, it is probable that the significant variation observed in the dorsal fin and girth scales is related to a difference in rate of development.

During the course of these racial studies, a large number of meristic features, including vertebrae, gill rakers, fin rays, and scales, and a large number of biometrical measurements, were considered for western subspecies fish from Western Australia, South Australia, and Tasmania. There is no evidence to suggest that the western subspecies is divisible into two separate breeding communities as suggested by Fairbridge (1950). Tagging experiments, and the elucidation of the life history of each subspecies (Malcolm, unpublished data), indicate that each of the subspecies comprises a single homogeneous population.

VI. Acknowledgment

The author wishes to thank Professor H. Waring of the University of Western Australia for providing laboratory facilities in the Department of Zoology during the course of these investigations.

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FACTORS INFLUENCING THE SETTLING OF THE PRINCIPAL MARINE FOULING ORGANISMS IN SYDNEY HARBOUR

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Summary

The macrofouling organisms most commonly encountered during intermittent plate exposures in Sydney Harbour over 10 years (1947–57) comprised a barnacle (mainly *Balanus* (*Balanus*) *amphitrite* var. *cirratus* Darwin), several serpulids and bryozoans (*Hydroides norvegica* Gunnerus, *Spirorbis* sp.; *Bugula neritina* L., *Bugula avicularia* L., *Watersipora cucullata* (Busk)), a mussel (*Mytilus planulatus* Lamarck), and an oyster (*Crassostrea commercialis* Iredale & Roughley). With the exception of the mussel, settlement was heaviest during the summer months. Surface water temperatures averaged from about 15°C in midwinter to 24°C in midsummer and were over 20°C for 6 months of the year. Two cases where freshwater dilution apparently affected biological populations are recorded. The effects of colour, surface texture, depth, aspect, and horizontal distance on settling were investigated using paired series of plates. The results were treated statistically and compared with those reported by others. It is suggested that during antifouling raft tests at this locality the control plates for any group of experimental plates need to be placed at the same site, same depth, facing the same way, and 5–10 ft apart horizontally. Providing the most common macrofouling organisms settling at the station were considered as a whole, this arrangement seemed to give a reasonably accurate assessment of their settling intensity at the test site.

I. INTRODUCTION

An attempt has been made here to outline the fouling conditions encountered at certain stations in Sydney Harbour (Fig. 1) between 1947 and 1957. Particular emphasis has been placed on determining the most abundant and persistent animal macrofouling organisms during these years, their settling periods, and how these could be quantitatively measured during raft tests of antifouling surfaces.

II. METHODS

Two sizes of immersion plates were used: 14 by 9 in. roughened and smooth black Bakelite or clear Perspex plates were immersed at constant depths of 3 ft 9 in. or 6 ft 9 in. below the raft at Garden Island; 4 by 3 in. roughened black Bakelite plates were fixed below mean low water spring level at the Spit, North Head, and Darling Harbour Stations. After monthly immersions these plates were dried and a $\frac{1}{2}$-in. border of fouling scraped off the edges. In the case of the 14 by 9 in. plates, the macroorganisms settling on the lower left quarter of the remaining area were counted on both sides (total area counted: 52 sq. in.). All the organisms on both sides of the 4 by 3 in. plates were counted ($17\frac{1}{2}$ sq. in.). Diatom, hydroid,

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and algal mats were only recorded qualitatively (since their dense growth form usually obscured their original settling sites) and are not considered here. Plates were immersed in dilute hydrochloric acid until all visible traces of previous settlement were removed before reimmersion.

III. Principal Fouling Organisms

Histograms showing the relative intensity of the most commonly recorded macrofouling organisms at the Garden Island, Spit, North Head, and Darling Harbour stations are presented in Figures 2, 3, and 4. The relative densities of other species were too low to warrant inclusion in the present graphs but are recorded in the files of this laboratory.

Barnacles, tubeworms, bryozoans, and bivalve molluscs were most frequently encountered at these stations. The barnacles were mainly *Balanus* (*Balanus*) *amphitrite* var. *cirratus* Darwin, *Balanus* (*Balanus*) *amphitrite* var. *communis* Darwin, and *Balanus Balanus trigonus* Darwin. Where identification of newly settled barnacles was possible on the 1956 Garden Island plates, 13,218 were found to be *cirratus*, 253 *communis*, and 35 *trigonus*. The tubeworms were *Hydroides norvegica* Gunnerus and two unidentified species of *Spirorbis* (one dextral, the other sinistral). The latter settled in approximately equal proportions during any given month and are treated jointly here. The bryozoans were the erect *Bugula neritina* L., *B. avicularia* L. (mainly treated jointly), and the encrusting *Watersipora cucullata* (Busk). Bivalve molluscs were represented by the mussel *Mytilus planulatus* Lamarck and the oyster *Crassostrea commercialis* Iredale & Roughley. Although these organisms dominated the fouling at any given station one or more may have been poorly represented. Thus *Mytilus* and *Crassostrea* were common at the Spit but were scarcely recorded at Garden Island, whilst the reverse held for *Spirorbis* and *Bugula* sp. (see Figs. 2 and 3).

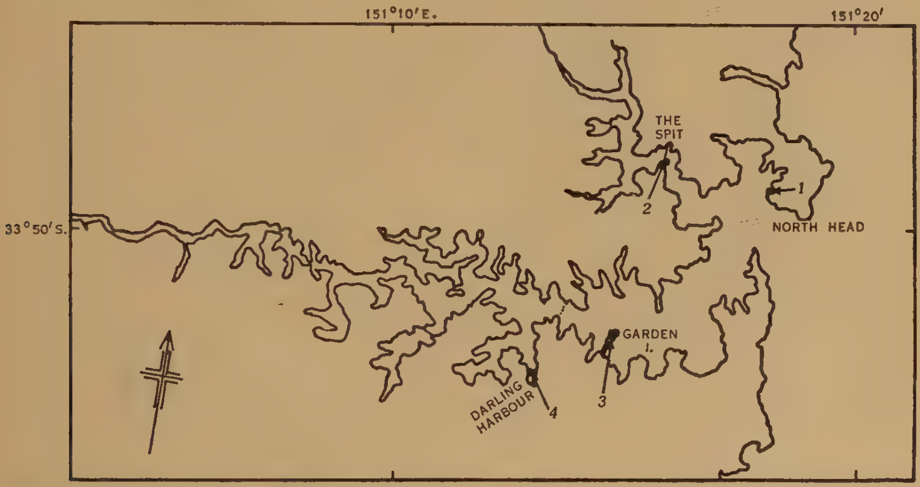

Fig. 1.—Map of Sydney Harbour (Port Jackson) showing location of plate exposure stations. Direct distance in miles from *1* to *2*, 2·3 miles; *2* to *3*, 4 miles; *3* to *4*, 1·8 miles.

IV. SETTLEMENT SEASONS AND THE EFFECT OF WATER TEMPERATURES AND CHLORINITY

(*a*) *Effect of Water Temperatures*

Water temperatures were taken at the surface at 1 p.m. at Garden Island (Table 1, p. 36). The values are slightly higher than those quoted by Fischer (1940) for Sydney Harbour, which were based on daily observations taken at 9 a.m. for 10 years. The different time of observation may account for the temperature differences. At Garden Island (Fig. 5) the winter months of June–August showed an average temperature of approximately 15–16°C which gradually rose to 23–24°C in the summer months of January–March. For 6 months of the year (November to April) the temperature was above 20°C and fouling settlement was at its heaviest during this period.

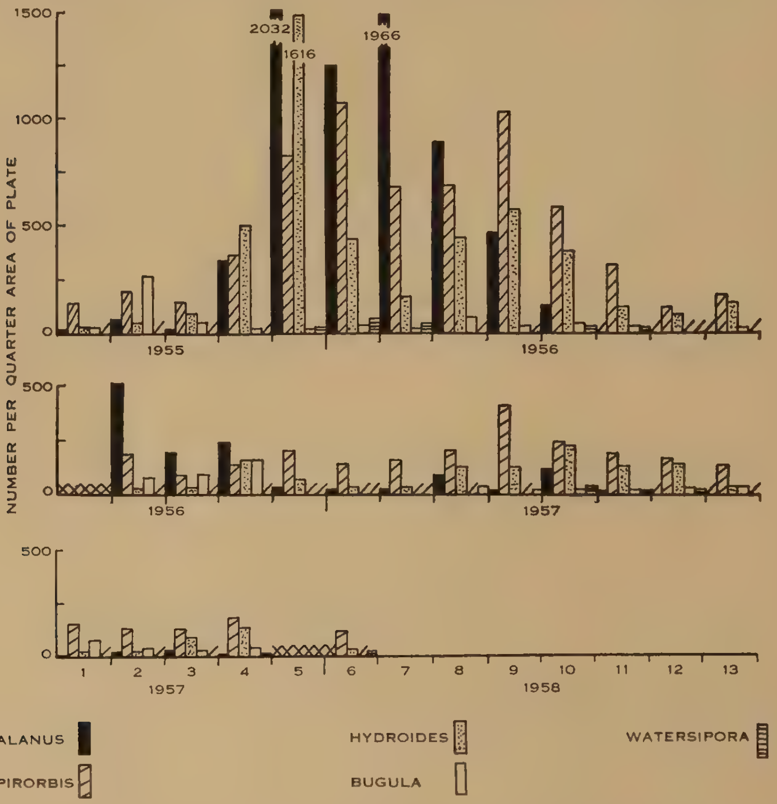

Fig. 2.—Average settling counts for periods of 4 weeks commencing on August 1, 1955, at the Raft station, Garden Island. Averages of one-quarter area of following 14 by 9 in. plates at 3 ft 9 in. or 6 ft 9 in.: 31.viii.55–16.viii.57, four plates (one rough, one smooth black Bakelite; one rough, one smooth clear Perspex); 29.ix.56–4.vii.57, 12 rough black Bakelite plates; 1.viii.57–16.i.58, six rough black Bakelite plates. ×, no record; /, no settling.

At the Spit and North Head stations *Mytilus* settled mainly in the spring (Fig. 6), settlement ranging from June to December and appearing to be more common in October. *Balanus* settlement ranged from October to April and reached a peak near midsummer (January). *Hydroides* reached its peak later during autumn (April); and although its settling season appears to be longer than those of the other organisms shown, this effect is due to its particularly heavy 1950 settlement which raised the 5-year average. In other years the range of settling was not nearly as extensive as this figure makes it appear. *Crassostrea* settlement extended from

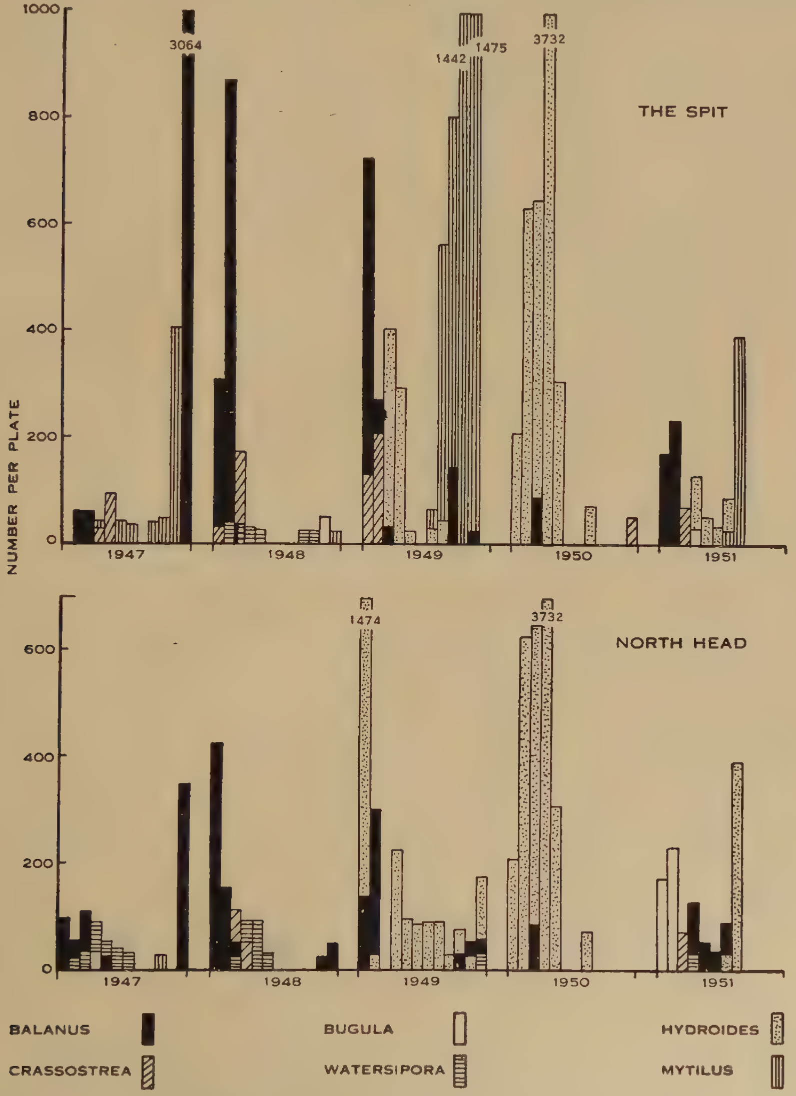

Fig. 3.—Monthly settling records at the Spit and North Head stations over 5 years (1947–51). Total counts 4 by 3 in. rough black Bakelite; no plates lost in this series.

December to June, slight peaks appearing in December, February, and April. *Watersipora* occupied much the same range.

The main settling season coincided, except for *Mytilus*, with the higher water temperatures (above 20°C) that occurred in late spring, summer, and autumn (November to May) but the intensity of settlement varied from year to year. As shown in Figure 3, *Balanus* was low in the counts in 1947, rose in 1948, and declined through 1949 to 1950 whilst *Hydroides* (Figs. 3 and 4), negligible in 1948, became prominent in 1949 and particularly in 1950. The same general trends were apparent in a separate series of similar plates exposed at fortnightly intervals during this period and were substantiated by docking reports over this period.

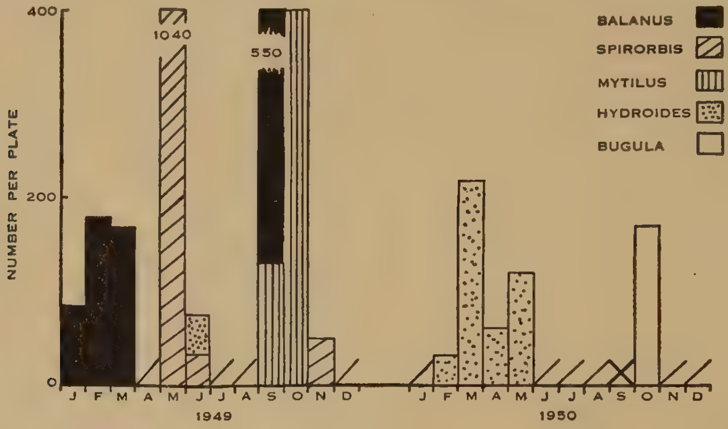

Fig. 4.—Monthly settling records, Darling Harbour station over 2 years (1950–51). Total counts 4 by 3 in. rough black Bakelite: ×, no record; ⁄, no settling.

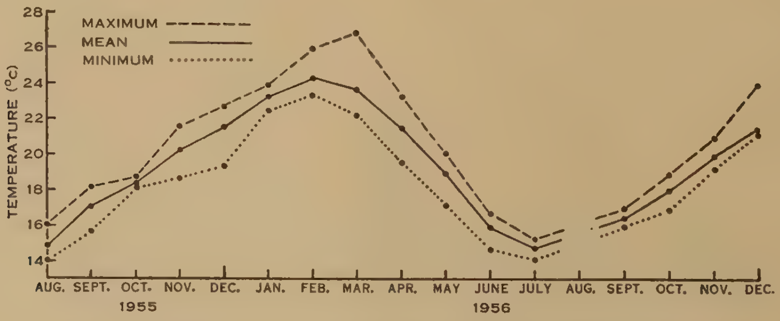

Fig. 5.—Surface water temperatures, Garden Island (from Table 1).

(*b*) *Effect of Variations in Chlorinity*

Chlorinity estimations were used to determine the salinity of surface seawater samples taken at Garden Island and these were compared with rainfall figures, the condition of adult fouling organisms, and effects on settling larvae.

Chlorinity values remained about 18–19‰ over most of this period (Table 1). These values are apparently normal for this locality and do not differ significantly from those of the open ocean. However, low monthly averages of 14·07‰ and 14·84‰ were recorded in February and March 1956, owing to exceptionally heavy rainfall during these months. According to Weather Bureau rainfall records (Fig. 7), 20·83 in. fell during February 1956 as compared with an average February figure of 3·01 in.; 14·21 in. fell in March 1956 compared with a 4·27 in. average. This rainfall, the second heaviest experienced during any month over at least the previous 13 years, had an effect on adult fouling organisms. On February 27, 1956, numerous barnacles, bryozoans, and tunicates were observed dead intertidally in several parts of the Harbour. A much heavier mortality was observed in two adjacent inlets (Botany Bay and Port Hacking). The chlorinity figures recorded during the preceding 17 days at Garden Island were very low (Table 2) and, although the depth to which dilution occurred and the effects of tidal movement were not determined, it has been recorded (C.S.I.R.O. Aust. 1956) that the "dilution of New South Wales coastal waters by fresh waters reached a maximum (for C.S.I.R.O. records of the preceding 14 years) in March 1956 when diluted coastal waters down to a depth of about 20 m were recorded from Evans Head to the Eden stations. Off the north coast of New

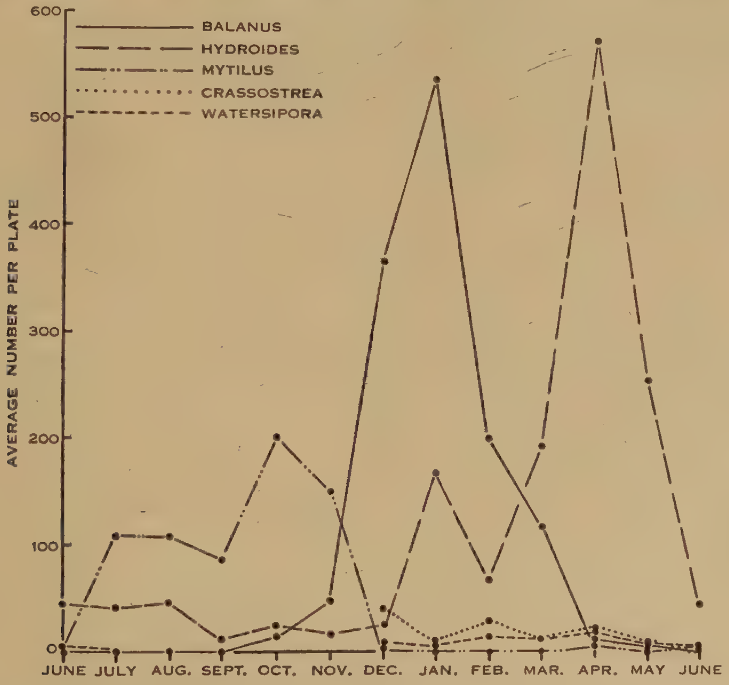

Fig. 6.—Average settling seasons of principal macrofouling organisms in Sydney Harbour over 5 years (1947–51). *Watersipora* from North Head alone, rest averages from Spit, North Head, and Darling Harbour stations. Total counts 4 by 3 in. roughened black Bakelite, counts below 20 per species per month not included in averages.

South Wales the dilution in this month corresponded to about a 15 per cent. introduction of river water."

Although this decrease in salinity caused mortality amongst adults (and probably further afield than noted here) the settling of larvae at Garden Island (Fig. 2) did not appear to be seriously affected. However, settlement was comparatively less in the following seasons and this could be due to the severe mortality that the adult population suffered in early 1956, and from which they may still be recovering. Current records of settling (not included in Fig. 2) are still low at this station.

TABLE 1

MONTHLY TEMPERATURES AND CHLORINITY RECORDS

Surface values, Point station, Garden Island, August 1955–December 1956

Year	Month	Temperature (°C)				Chlorinity (‰)			
		Av.	Max.	Min.	Observations per Month	Av.	Max.	Min.	Observations per Month
1955	Aug.	14·8	16·0	14·0	22	19·10	19·60	18·80	22
	Sept.	17·0	18·2	15·7	19	19·15	19·54	19·00	19
	Oct.	18·3	18·7	18·1	7	19·30	19·70	18·91	7
	Nov.	20·2	21·5	18·6	18	18·90	19·39	16·75	18
	Dec.	21·5	22·6	19·3	13	18·30	18·60	17·60	13
1956	Jan.	23·2	23·8	22·4	8	18·78	19·21	18·32	10
	Feb.	24·2	25·8	23·2	11	14·07	18·20	9·47	15
	Mar.	23·6	26·7	22·1	18	14·84	17·56	11·29	21
	Apr.	21·4	23·1	19·5	19	18·47	18·99	17·58	19
	May	18·9	20·0	17·1	23	18·79	19·05	18·21	23
	June	15·9	16·6	14·6	20	18·27	19·02	16·88	20
	July	14·7	15·3	14·1	22	18·73	19·02	18·14	22
	Aug.	*	*	*	*	18·92	19·09	18·37	23
	Sept.	16·4	16·9	15·9	9	19·28	19·34	19·15	9
	Oct.	17·9	18·8	16·9	19	19·29	19·40	19·07	17
	Nov.	19·7	20·3	19·2	16	19·50	19·80	19·37	6
	Dec.	21·2	23·8	21·0	8	19·56	19·62	19·48	8

* No record.

Rather similar circumstances were noted in June 1950 when the heaviest rainfall for any month in the 13-year period considered here (27·83 in. compared with a June average of 3·24 in.) decreased salinities on June 14 at the Spit (3·13‰) and North Head (9·58‰), but not appreciably in coastal waters. At the Spit and North Head this was followed by practically no settling of fouling organisms for approximately 6 months (Fig. 3). The settling of *Mytilus*, which was expected to take place at the Spit sometime during this period, did not eventuate and the settling of *Hydroides* terminated abruptly (as it did also at Darling Harbour, Fig. 4). Since *Hydroides* settlement took place at the Spit and North Head stations during these months in both the preceding and following years, it seems unlikely that this cessation was due to natural termination of the settling season. The evidence from

Garden Island and these stations, though not extensive, is sufficient to suggest that abnormally heavy rainfall may have an effect on fouling populations in Sydney Harbour.

V. The Assessment of Fouling in Raft Tests

During raft tests of antifouling paints it is desirable to ascertain the kind, intensity, and duration of fouling settling at the site over the immersion period. At the Raft station, Garden Island, there appeared to be differences in the settling on control plates only a few yards apart, apparently associated with variations in depth, illumination, and horizontal distance apart. Series of paired plates were immersed at monthly intervals from September 1956 to May 1957 to test the effects of these variables.

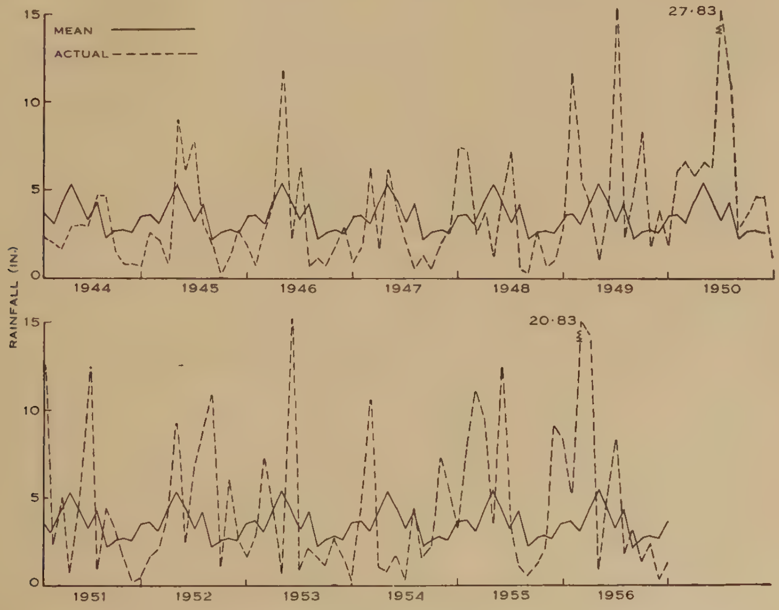

Fig. 7.—Mean and actual monthly rainfall for Sydney Harbour and environs for 13 years (1944–56). From Weather Bureau records, Commonwealth of Australia.

(a) *Nature of the Control Surface*

Control plates were used which offered highly favourable conditions for settlement. Exact individual matches for the various antifouling paints were not attempted. It would be difficult, for example, to match the colour of a cuprous oxide antifouling paint which may be red, yellow, grey, green, or blue, depending on its history. Duplication of surface texture presents similar problems. Of the surfaces tested (Table 3 shows some of the results) roughened black Bakelite was selected as being the most favourable; for more precise results the amount of roughness would need to be standardized. Counts of settling on such favourable surfaces, provided they were properly positioned, could be expected to give a reliable index of the potential fouling in the immediate vicinity of antifouling plates during immersion.

(*b*) *Variations in Settling Intensity with Depth*

In these tests 14 by 9 in. roughened black Bakelite plates were suspended in standard frames (Laurie 1955, fig. 3) so that the only apparent difference was in depth. One plate of each pair was suspended at a constant depth of 3 ft 9 in. and the other at 6 ft 9 in., these being the upper and lower levels of paint trials at the Raft station. The results are given in Table 4. Although there appears to be no significant difference in the settling at these depths of *B. avicularia* and *Watersipora* there are significant differences for the other four organisms considered. *Balanus* was more common on the deeper plates by a ratio of 3·7 : 1 whilst the reverse held, to a lesser extent, for *Spirorbis* (1·8 : 1), *B. neritina* (1·7 : 1), and *Hydroides* (1·3 : 1). This suggests that controls and experimentals should be placed at the same depth.

Table 2

DAILY TEMPERATURE AND CHLORINITY RECORDS FOR FEBRUARY 1956 DOWNPOUR

Date	Rain (in.)	Chlorinity (‰)
10	7·56	16·65
11	3·67	*
12	0	*
13	0·40	9·47
14	0	9·58
15	0	11·90
16	0	13·45
17	0·37	*
18	0·84	*
19	1·98	*
20	0·82	12·58
21	1·72	13·35
22	2·83	11·83
23	0·19	12·52
24	0·22	14·65
25	0·05	*
26	0	*
27	0·04	15·89
28	0·07	16·37
29	0·30	16·61

* No record.

(*c*) *Variations in Settling Intensity with Illumination*

The plates under the raft (which was moored at both ends and could not swing freely) were exposed to different light intensities. The north-facing sides of the plates developed more plant and less animal life than the southern sides. In the Southern Hemisphere north-facing aspects are sunny and southern aspects shaded; they are referred to here as "light" and "dark" sides respectively. The animals considered (Table 5) settled significantly more abundantly on the dark sides than on the light, except for *Watersipora* where the results were only possibly significant ($P = 0\cdot05$–$0\cdot1$). It should be noted that these differences cannot be entirely attributed to photonegative behaviour by the settling larvae since the development of dense plant mats on the lighted side considerably decreased the area of plate available to them. It seems that comparisons of counts, for example, on the dark side of one plate with the light side of another would be invalid, and that it is necessary to compare the corresponding sides of two plates, or the totals for the two opposite sides of one plate with those of the other. This procedure has been followed here where applicable.

TABLE 3

EFFECT OF COLOUR AND SURFACE TEXTURE ON SETTLING

14 by 9 in. plates, at 3 ft 9 in. or 6 ft 9 in. depth, facing same way, less than 3 ft apart; $\frac{1}{4}$ area of each plate counted ×4 to give total settlement. Raft station, Garden Island. 28 day exposures

End of Immersion Period	Plate Type	Numbers Settling per Plate			
		Balanus	*Hydroides*	*Spirorbis*	*Bugula*
15. ii.57	Black Bakelite, roughened	9812	458	2611	9
	smooth	4914	463	1632	19
	Clear Perspex, roughened	469	157	214	8
	smooth	40	262	936	21
14.iii.57	Black Bakelite, roughened	3280	2698	2940	448
	smooth	1193	1264	1648	69
	Clear Perspex, roughened	1168	477	454	44
	smooth	2678	69	459	38
26. x.56	Black Bakelite, roughened	30	442	970	254
	smooth	8	0	426	81
	Clear Perspex, roughened	24	166	59	49
	smooth	21	165	256	347
9. v.57	Black Bakelite, roughened	1280	988	1868	316
	smooth	840	1684	2480	40
	Clear Perspex, roughened	63	176	226	0
	smooth	32	58	126	0
Averages	Black Bakelite, roughened	3600	1146	2097	257
	smooth	1739	853	1299	52
	Clear Perspex, roughened	431	244	238	25
	smooth	693	136	444	101

(*d*) *Horizontal Variations in Settling Intensity*

It is apparent from the foregoing that if two plates were placed at the same depth and facing the same way, they should, providing they were not too far apart, experience much the same kind and intensity of fouling. Tests were made at horizontal distances of 10 ft and 5 ft (the limits of the testing positions) to see if this was approximated. The results (Table 6) show that in the 12 sets of cases considered there were significant differences in only three, viz. *B. avicularia*, *Balanus*,

TABLE 4

EFFECT OF DEPTH ON SETTLING

14 in. by 9 in. roughened black Bakelite plates, facing same way, shallow plate at 3 ft 9 in., deep vertically below at 6 ft 9 in.; ¼ area of plates counted and compared for the same sides at the two depths, ×4 to give total settlement. Raft station, Garden Island; 28 day exposures

Organism	Total Settling on		$n-1$	t	Significance Level* P
	Shallow Plates	Deep Plates			
Balanus sp.	3007	11188	43	5·057	<0·001
Spirorbis sp.	13168	7444	51	5·272	<0·001
Hydroides norvegica	6091	4757	51	2·379	<0·05
Bugula avicularia	1586	1221	43	1·882	n.s.
Bugula neritina	1458	854	42	2·793	<0·01
Watersipora cucullata	476	245	35	1·911	n.s.

*Here, and in Tables 5 and 6, $P<0\cdot001$ is rated as highly significant, $P = 0\cdot01$–$0\cdot05$ as significant, $P = 0\cdot05$–$0\cdot1$ as possibly significant and $P>0\cdot1$ as not significant (n.s.). n is the number of plates compared.

TABLE 5

EFFECT OF ILLUMINATION ON SETTLING

14 in. by 9 in. roughened black Bakelite plates facing same way at 3 ft 9 in. or 6 ft 9 in. North sides lighted, south sides dark. For each plate ¼ area on each side counted and compared, ×4 to give total settlement. Raft station, Garden Island; 28 day exposures

Organism	Total Settling on		$n-1$	t	P
	North Side (Light)	South Side (Dark)			
Balanus sp.	4186	8377	87	4·705	<0·001
Spirorbis sp.	7392	10113	87	3·903	<0·001
Hydroides norvegica	3045	6505	87	5·140	<0·001
Bugula avicularia	1027	1836	80	5·097	<0·001
Bugula neritina	933	1580	82	2·786	<0·01
Watersipora cucullata	291	464	57	2·06	>0·05

and *Spirorbis*. It follows that if one of these two plates was replaced by an experimental antifouling plate and the other used as a control, the counts obtained from the latter would give a reasonable approximation of the kind and intensity of potential fouling that the experimental plate was resisting.

VI. DISCUSSION

Comparisons can be drawn between the foregoing data and those recorded by others. The results of Coe and Allen (1937) based on a 9-year (1926–35) study at La Jolla, California, are particularly appropriate since the latitude and temperature of that locality is similar to that of Sydney Harbour. Coe and Allen considered there were seven principal groups of sedentary organisms present at La Jolla; i.e. algae (mainly *Ectocarpus* and *Herposiphonia* sp.), diatoms (60 sedentary species), hydroids (nine species), barnacles (mainly *Balanust intinnabulum californicus* Pilsbry), bivalves (*Ostrea lurida* Carp.), bryozoans (16 species including *Bugula neritina*), and serpulids (three species including *Spirorbis* sp.). The results were based on volumetric determinations of the amounts of the organisms settling on wood-cement, wood, and glass plates for 2 or 4 week periods. As noted earlier, quantitative determinations of diatoms, algae, or hydroids were not attempted in the present study because of the difficulty of discerning the original settling points in such dense growths. Coe and Allen also comment on this difficulty. In both localities (excluding the hydroids) barnacles, serpulids, bryozoans, and bivalve molluscs can be considered as constituting the most common and persistent of the animal macrofouling organisms.

TABLE 6

EFFECT OF HORIZONTAL DISTANCE APART ON SETTLING

14 in. by 9 in. roughened black Bakelite plates at 3 ft 9 in. or 6 ft 9 in., facing same way. One plate of each pair 5 ft or 10 ft apart horizontally; $\frac{1}{4}$ area of both sides of each plate counted and added and compared with that of partner plate, ×4 to give total settlement. Raft station, Garden Island; 28 day exposures

Organism	Total Settling at Distance of		$n-1$	t	P
	0 ft	x ft			
(*a*) At $x = 10$ ft apart					
Balanus sp.	9305	9760	61	0·301	n.s.
Spirorbis sp.	10303	10227	51	0·099	n.s.
Hydroides norvegica	6784	5281	53	1·650	n.s.
Bugula avicularia	913	626	31	2·338	$<0{\cdot}05$
Bugula neritina	932	946	29	0·077	n.s.
Watersipora cucullata	323	423	35	0·909	n.s.
(*b*) At $x = 5$ ft apart					
Balanus sp.	8305	5466	47	2·640	$<0{\cdot}05$
Spirorbis sp.	12313	9138	56	3·069	$<0{\cdot}01$
Hydroides norvegica	5819	5354	55	1·016	n.s.
Bugula avicularia	854	979	30	0·840	n.s.
Bugula neritina	953	779	32	1·215	n.s.
Watersipora cucullata	331	345	26	0·115	n.s.

The Sydney Harbour results emphasize that settlement counts merely give information on the body of water immediately around the collecting surface. There are not only broad differences between stations (Figs. 3 and 4) but also distinct differences associated with the nature, arrangement, and depth of the collecting surfaces over distances of only a few yards at a given station (Tables 3, 4, and 5). Amongst the more obvious factors involved are (i) current speed (since a fast current will pass more volume of water per unit time over a plate and give more larvae the chance of settling there), (ii) proximity of breeding adults (particularly those releasing larvae that settle within a few hours of liberation, e.g. *Bugula* and *Watersipora*), (iii) depth at which the plate is suspended (see Table 4), and (iv) the settling reactions of the larvae themselves to the surfaces provided, the complexity of which is indicated in the raft tests (Tables 3, 4, and 5).

Despite these variables, the use of a number of stations over at least several years has certain advantages. It does, for instance, provide positive distribution records of many organisms and their settling seasons. The characteristics of individual stations can be ascertained (e.g. the relatively heavy settlement of *Mytilus* at the Spit and the reverse at North Head, as shown in Figs. 3 and 4) and these can be distinguished from more general trends (e.g. the relatively heavy 1950 settlement of *Hydroides* at all three stations, Figs. 3 and 4). The underlying causes of the latter, apparently long term, fluctuations are not clear. Coe and Allen (1937) also noted "that each of the nine years has shown certain peculiarities both in the periodicity and in the abundance of some of the organisms" but pointed out that these fluctuations were relatively inconspicuous when the combined observations for the entire period were summarized. Their graph shows that the mean peak settlement of *Ectocarpus* was 6 weeks earlier in the 3 years ending 1935, as compared with the 9-years mean ending 1935; and that *Balanus* was about 6 weeks earlier during this period. Also, there was about 25 per cent. more "volume" of *Ectocarpus* and 25 per cent. less of *Balanus* in this period as compared with the long term mean. Similar differences are apparent in the Sydney Harbour data and it appears that a variation of 1–2 months either way in the onset of the main settling season, and 25 per cent. variations in abundance can be expected during short term exposure series of 1–3 years. The Sydney Harbour data suggest, however, that in this particular locality fresh water dilution can have catastrophic effects on the adults or settling larvae, or both, which may have repercussions on the intensity of settling during the following years.

Redfield and Deevy (1952) have presented graphs of the water temperatures and settling seasons of sedentary organisms for many parts of the world. In "tropical waters" (temperature range 20–30°C) the settling of many organisms is continuous throughout the year but in "temperate waters" (temperature range 10–20°C) settling seems largely confined to the warmer months of the year. Unfortunately many of the comparisons are only at the generic or higher levels but in *Bugula neritina* it is evident that the length of the breeding season is proportional to the increase in temperature, becoming continuous at about 25°C. Sydney Harbour appears to occupy an intermediate position. The main settling periods (except for *Mytilus*) coincide with the higher water temperatures (Figs. 5 and 6) as in temperate waters but there is evidence that although *Hydroides norvegica* and *Watersipora cucullata* follow this trend, they also settle continuously throughout the year, as might be expected in tropical conditions (Wisely 1958*a*, 1958*b*). The position of the other organisms discussed here has not yet been determined.

The comparisons between settling on rough and smooth surfaces and on black or clear plates (Table 3) tend to substantiate the findings of others. Visscher (1927) found that at first light coloured unglazed tiles showed substantially less settlement than dark coloured ones, and Edmondson and Ingram (1939) showed that white and green coloured paints and glass were more effective in discouraging settlement than darker ones. In both cases little difference was observed, regardless of colour, after 2 or 3 months exposure, apparently owing to slime formation. Corlett (1948), however, observed no significant difference in the settlement on black, red, or white painted surfaces exposed for 1–5 weeks in the Mersey Estuary. He considered that this was due to lack of light penetration in these muddy waters, and to rapid discolouration of light-coloured surfaces with brown slime. In Sydney Harbour *Balanus*, *Hydroides*, *Spirorbis*, and *Bugula* showed, except for a few cases (Table 3), much higher counts on the dark plates. Settlement was also substantially heavier on the roughened as contrasted with smooth, black, and clear plates for all four organisms, except for *Spirorbis* and *Bugula* on the clear plate series. Here, for some unknown reason, settlement was heavier on the smooth series. In this connection Corlett (1948) reported similar settlement on unglazed red and white tile surfaces by the hydroids *Tubularia indivisa* L. and *Laomedea flexuosa* Hincks, the bryozoan *Pedicellina cernua* (Pallas), and the barnacle *Balanus improvisus* Darwin, but noted that of these only *T. indivisa* settled on glazed white tile surfaces alongside. This evidence hints at differences in larval reactions to surface texture.

Depth appears to be an important factor in settlement. The results (Table 4) showed that *Balanus* settled much more abundantly at 6 ft 9 in. than at 3 ft 9 in.; that *Spirorbis*, *Hydroides*, and *Bugula neritina* evidently preferred the shallower level; and that *B. avicularia* and *Watersipora* apparently showed no preferences. McDougall (1943) obtained very similar results with *Balanus eburneus* Gould. He noted that on plates suspended below a raft, settlement increased steadily with depth down to 6 ft, the lowest level tested.

Comparison of settlement on the light and dark sides of the same plates (Table 5) showed that five out of the six organisms settled significantly on the dark side. Gregg (1945) showed for cyprid larvae that a decrease in general illumination around the collecting surface was accompanied by an increase in settlement, which led him to suggest that "shading" acted as a stimulus which brought about favourable physiological conditions for the attachment of these larvae. On sunny days the dark sides of the above plates were shaded; but little can be added, aside from the observations given in Table 5.

It was found (Table 6) that there was close similarity in the settling on pairs of plates 10 or 5 ft apart horizontally when the other variables (colour, surface texture, depth, and aspect) had been equalized. Significant differences were only noted in three out of the 12 sets of data, i.e. in *Balanus*, *Spirorbis*, and *B. avicularia*. Small differences in illumination or direction and intensity of water currents may have given one of a pair of plates a slight advantage in encountering settling larvae. In other species of two of these genera, i.e. in *Balanus balanoides* (L.), *B. crenatus*

Bruguiere, *Spirorbis borealis* Daudin, and *S. pagenstecheri* Quatrefages, Knight-Jones (1951, 1953) has suggested that the larvae have a marked tendency to settle around previously settled individuals of their own species ("gregariousness") and it follows that initial colonization of a surface by a few individuals could be followed rapidly by heavier settlement. It is not yet known, however, if the larvae of these Sydney Harbour species show similar reactions.

The results of the raft tests are sufficient to suggest that considerable errors can be involved in quantitative raft testing unless the control plates, which should preferably present highly favourable and uniform surfaces to settling larvae, are placed at the same site, same depth, facing the same way, and 5–10 ft apart horizontally from the experimentals. It also seems necessary to consider the most abundant macrofouling organisms settling at the site collectively. Monthly counts of the settling appearing on control plates exposed along these lines could be expected to give a reasonably accurate assessment of the kind and intensity of potential fouling settlement that the experimentals were exposed to during immersion.

VII. Acknowledgments

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REPRODUCTION IN AUSTRALIAN PEARL OYSTERS (LAMELLIBRANCHIA)

V. PINCTADA FUCATA (GOULD)

By D. J. Tranter*

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Summary

Pinctada fucata, in common with *P. albina* and *P. margaritifera*, is hermaphrodite. The gonad develops in a series of phases, in which germ cells are formed anew from indifferent "stem cells" which remain after spawning. Each phase is unisexual, but sex may change from phase to phase. There is a tendency towards protandry, but this is less marked than in *P. albina*. The percentage of individuals in female phase increases until middle life, by which time the sexes are equally common. Both protandric and protogynic sex-changes have been recorded in the field and, on one occasion, a bisexual, transitional condition was observed in gonad sections. The evidence shows that sex change is not restricted to the wintering period.

Primary gonad differentiation begins 2–3 months after spat settlement, and within 6 months sexual maturity is reached. Frequently, there is a second phase of gonad development towards the end of the first year.

The typical adult breeding cycle consists of: a period of gonad differentiation from September to November; a spawning period from December to May; and a resting period from June to August. During the spawning season, there are usually two periods of maximum intensity: January–February ("summer spawning") and April–May ("autumn spawning"), the latter being the more consistent of the two. However, lesser spawnings occur outside the major spawning season, and spatfalls have been recorded throughout the year.

The macroscopic and histological structure of the gonad is similar to that of *P. albina* and *P. margaritifera*. The following points are noted: gonad colour is an unreliable indication of sex; the white mantle layer covering the gonad is predominantly mucoprotein, and is probably concerned with shell secretion; there are no yolk nuclei visible in the cytoplasm of the oocyte, as in *P. margaritifera*; activation of the ripe oocyte takes place within the gonad follicles immediately prior to spawning; as in *P. albina* spawning is frequently incomplete, and phagocytosis plays a major role in the resorption of unspent gonad products; the haploid chromosome number is six.

I. Introduction

Prior to Hynd (1955), *Pinctada fucata* (Gould) was known as *P. vulgaris* (Schumacher). It is the "lingah" pearl oyster of the Ceylon and Persian Gulf pearl fisheries, and is distributed throughout the Indo-Pacific region. In Australia, the species occurs between Shark Bay on the west coast, and Port Hacking on the east coast, and coexists with *P. albina* (Lamarck) in intertidal situations with a suitable substratum; the two share the same ecological niche and, in fact, are known jointly in Moreton Bay as "quompi", and at Groote Eylandt as "ilycrumba".

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The Japanese pearl oyster, referred to in the literature as *P. martensi* (Dunker), is closely allied to *P. fucata*. Since there is information concerning its biology, it is important to establish the mutual relationship more precisely. Jameson (1901) considered that the Japanese population would eventually prove to be "a local form" of the present species, and Prashad and Bhaduri (1933) agree with this. The present author has also examined specimens from Japan and found them to fall within the range of variability of *P. fucata*; therefore the Japanese pearl oyster is here referred to as *P. fucata*.

In contrast with the "silverlip", *P. maxima* (Jameson), and "blacklip", *P. margaritifera* (Linnaeus), the shell of *P. fucata* is of no commercial value, the oyster being fished for its pearls. In the Ceylon and Persian Gulf areas, the species has been fished at irregular intervals for centuries; in Japan, it forms the basis of a profitable pearl culture industry.

The biology of *P. fucata* has already received attention, in particular by Herdman and Hornell (1903, 1904, 1906). The present paper is concerned with the reproductive habits of the species in Australia, and is the final report in the current series. The investigation on *P. maxima* will be published by J. S. Hynd who, in 1949, initiated the whole series of investigations as part of a general study on Australian pearl oysters.

II. Materials and Methods

In general, the methods used in this investigation parallel those adopted for *P. albina* (Tranter 1958*a*, 1958*b*, 1958*c*) and *P. margaritifera* (Tranter 1958*d*). Routine sampling was at fortnightly intervals over the 3-year period 1953–55 (sample size, 25). Material was chiefly from collectors in the Thursday Island area, supplemented at times by collections from Crab Island (for map, see Tranter 1958*a*) and, occasionally, Groote Eylandt. The Moreton Bay population was examined in March and April 1955. The following recordings were taken: heel depth, dorsoventral measurement, sex, and macroscopic gonad stage. Selected gonads from the routine samples, and the whole of the Banda Rock buoy material of October 1955, were fixed and sectioned (total number, 100). These were classified on histological criteria, according to the system of stages adopted for *P. margaritifera*, which is a modification of that designed for *P. albina* (Tranter 1958*b*). Records of spat settlement on plates of standard area were made available by J. S. Hynd.

In addition to the above observations, it has been possible, with this species, to follow, for the first year and a half, the reproductive history of a particular spat group; these observations have yielded precise information not otherwise obtainable. Further, they provide a comparison with data obtained by less direct methods (as above), and are in this respect a test of the accuracy of those methods. Accordingly, the two sets of observations are presented independently and the respective conclusions then compared. The material referred to consists of 511 spat which settled on collectors at Possession Island between November 1955 and March 1956. The group was first sampled in March 1956, and then at monthly intervals from August 1956 to August 1957 (sample size, 20). Altogether, 270 gonads were examined, and these were later sectioned.

III. STRUCTURE AND HISTOLOGICAL APPEARANCE OF THE GONAD

The gonad, first described in detail by Herdman and Hornell (1904), resembles in most respects that of *P. albina* (Tranter 1958*a*) and *P. margaritifera* (Tranter 1958*d*). However, gonad colour is here an unreliable indication of sex and, although the female gonad is most frequently yellow as in other species, the male is as often orange as it is cream (the usual testis colour of pearl oysters). The orange colour is not that of the contained gametes, but is in the external epithelium.

There is often a white mucoid layer covering that part of the mantle overlying the gonad; this is frequently so well developed that the gonad is completely obscured from view. Herdman and Hornell (1904) have remarked on this also. The variability in the development of this layer, its proximity to the gonad, and the fact that it has been referred to as a glycogen layer (Ojima 1952), suggests that the structure may be concerned with gonad development. It was therefore investigated. There is no reaction with standard glycogen stains or with sudan IV, and chemical analyses confirmed that there is very little glycogen or fat present; nitrogen, however, is a major constituent. This suggests that the substance is largely protein. The layer stains heavily with Bismarck brown (Plate 1, Fig. 4) which is indicative of mucoprotein. It is considered, therefore, that the structure is not concerned with gonad development, but more probably with shell secretion.

The histological structure of the gonad is similar to that of *P. albina* and *P. margaritifera*. Some features, however, require comment: there are no yolk nuclei to be seen in the cytoplasm of the oocyte as there are in *P. margaritifera;* the ripe oocyte (Plate 1, Fig. 1) becomes activated immediately prior to spawning and meiosis proceeds to the metaphase of the first reduction division (Plate 1, Fig. 2); maturation continues after fertilization, upon which the reduction divisions follow in rapid sequence (Plate 1, Fig. 9); spawning is often incomplete (Plate 1, Fig. 5) and, as in *P. albina*, phagocytosis plays a major role in the resorption of unspent gonad products.

Several aspects of germ cell maturation were seen more clearly in this material than in that from other species; these are shown in Plate 1. In Figure 6 of this Plate are primary spermatocytes in late diplotene; these have also been noted in *P. margaritifera* (Tranter 1958*d*) though never in *P. albina*. Plate 1, Figure 7 shows the difference in appearance between primary and secondary spermatocytes. The clearest spermatogonial metaphase yet encountered in pearl oyster gonads is shown in Plate 1, Figure 8; the chromosomal count (diploid) is 12. This may be compared with the haploid arrangement in Plate 1, Figure 9 which is a section across a fertilized egg showing the metaphase chromosomes of the future female pronucleus. This egg had been fertilized after spawning, and ingested with feeding currents.

IV. OBSERVATIONS ON THE GENERAL POPULATION

(*a*) *Growth Rate*

It is possible to tell whether a specimen is young, old, or middle-aged from such superficial characters as coloration, shell erosion and infestation, and vigour of growth processes. However, shell measurements allow a more precise estimation of age. The largest specimen of *P. fucata* observed by Hynd (1955) had a dorsoventral measurement of 9 cm and a heel depth of 10 mm; this may be regarded as a close approximation to the maximum size of the species.

Heel depth is the more reliable measure of age, since it shows a fairly regular rate of increase irrespective of environmental conditions. For instance, maximal dorsoventral measurement may be reached in less than a year, whereas heel depth increases for many years. This is shown in Table 1 where measurements of fast grown individuals are listed. These are from the hollow cylinder stem of navigation light buoys in the Torres Strait area (for map see Tranter 1958*a*), and are the largest specimens from each sample. In general, their dorsoventral measurement is as great as has ever been recorded; indeed, one specimen measured 9·7 cm. Nevertheless, their age is less than a year since the buoys are cleaned annually. The species lives at least 4 years (Malpas 1933); therefore this first-year growth in dorsoventral measurement is exceptionally fast. On the other hand, the average heel depth of these specimens is only one-fifth of the maximum and the valves are wafer-thin. Thus heel depth is the better measure of age. In young oysters, however, where rate of increase in dorsoventral measurement is fairly regular and where measurements of heel depth (to the nearest half-millimetre) are comparatively coarse, dorsoventral measurement can also be useful in age determination.

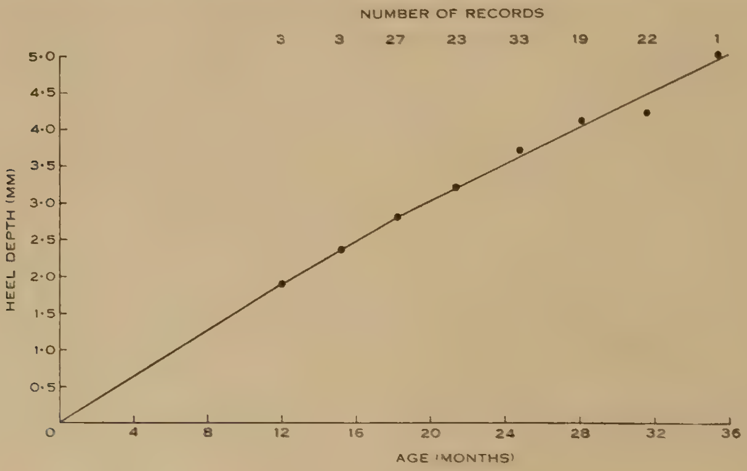

Fig. 1.—Growth rate of *P. fucata* in the heel depth dimension; the points plotted represent the mean growth of a number of tagged oysters over a period of time. The actual numbers measured are given above.

Continuous observation on individual tagged oysters indicate that a heel depth of 5 mm is reached in 3 years (Fig. 1). Buoy specimens (Table 1) reach 2 mm in less than a year. The exact figure could be arrived at only if it were known how soon spat settlement took place after the buoys were laid. The fact that these (largest) individuals have reached maximum size in the dorsoventral dimension suggests that they are, indeed, nearly 12 months old; this is supported by the fact that they have a common heel depth value (2 mm).

On these grounds, it is considered that a heel depth of 2 mm is rarely exceeded in the first year; the average figure is probably a little less than this, since the buoy specimens whose measurements are listed (Table 1) were the largest from each sample. There is the further possibility that, though heel depth does not reflect the superior growing conditions to the same extent as does dorsoventral measurement, the rate of heel depth increase in buoy material may, in fact, have been slightly greater than under more normal growing conditions.

To summarize, age may be estimated from heel depth. The evidence indicates that the average annual increment is 1·5–2 mm per year. Significant events in the life cycle, such as age at first maturity and change of sex, may now be related to age.

Table 1

SIZE OF LARGEST SPECIMENS FROM NAVIGATION LIGHT BUOYS EXPOSED FOR EXACTLY 12 MONTHS

Locality	Date of Cleaning	Size of Largest Specimen		
		Weight (oz)	Heel Depth (mm)	Dorsoventral Measurement (cm)
Marina Rock	October 1953	2	2	9·0
	October 1954	1½	2	8·4
Harrison Rock	July 1954	1½	2	6·9
Banda Rock	October 1954	2	2	9·0
	October 1955	1⅞	2	9·7

(*b*) *Breeding Season*

(i) *Seasonal Gonad Development.*—Regular observations over three complete years reveal a basic seasonal pattern of gonad development. The percentage frequencies of full and empty gonads per fortnightly sample of 25 are shown in Figure 2. The three annual cycles have the following features in common:

(1) Seasonal gonad development begins in September or October.

(2) Most gonads are ripe by December.

(3) There is a certain amount of spawning between December and April, but gonads fill again rapidly.

(4) During April, May, or June there is a major spawning.

(5) Few gonads are ripe from June to September.

However, the seasonal cycles differed from year to year in the following respects:

(1) In 1952–53, there was comparatively little spawning between December and April; from July to September there was appreciably more spawning than in other years.

(2) In 1953–54, there were minor spawnings in December and February and again the following August.

(3) In 1954–55, there was a major spawning in late January, February, and early March; there was little or no spawning between July and September; the major "autumn spawning" occurred a month later than in other years.

It is evident, therefore, that, whereas the autumn spawning is a regular occurrence, others vary in intensity from year to year. This could be in response to the varying environmental conditions. However, the evidence suggests that there may be a correlation between the intensity of a particular spawning and spawning behaviour in the past months. For instance:

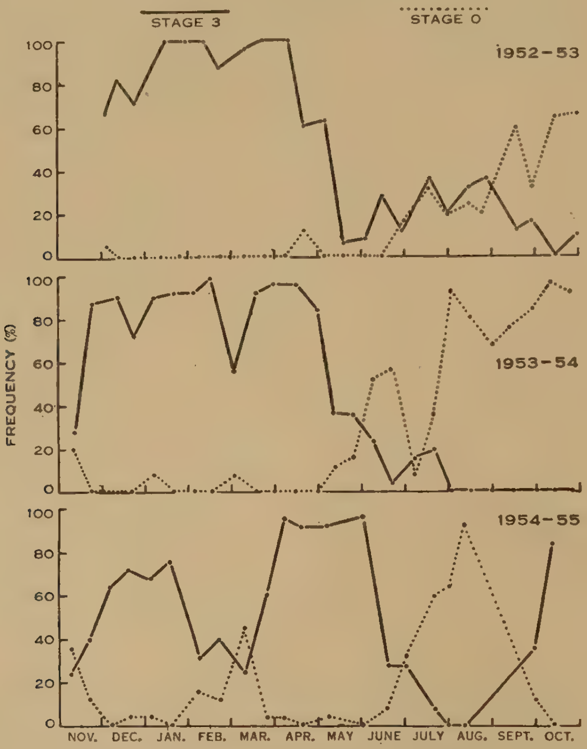

Fig. 2.—Seasonal gonad development as indicated by the percentage frequency of full (stage 3) and empty (stage 0) gonads in regular fortnightly samples of 25 adult oysters.

(1) When there is little summer spawning (as in 1952–53), there is appreciable gonad development and spawning the following winter; conversely, when the summer spawning is of major dimensions (as in 1954–55), there is little or no spawning the following winter; in this regard, 1953–54 occupies an intermediate position.

(2) The major summer spawning of 1954–55 was preceded by a prolonged wintering period.

These features could, however, be fortuitous and it would be necessary to observe breeding behaviour over a number of years to confirm whether or not there is such a correlation.

To summarize, the evidence indicates that the breeding cycle consists of: a resting period during the colder months; a period of gonad differentiation during spring and early summer; and a spawning season from midsummer to autumn. There is always a major spawning in autumn (April–June) and often an earlier one in February (summer spawning). In some years there are minor spawnings in winter.

TABLE 2

GONAD DEVELOPMENT OF PINCTADA FUCATA IN MORETON BAY

Date	Number Examined	Frequency (%)			
		Stage 3	Stage 2	Stage 1	Stage 0
11.iii.55	131	63	32	4	1
25.iv.55	366	78	17	4	1

There is a certain amount of evidence which suggests that south Queensland populations may have similar breeding habits. This consists of observations on the gonad condition of 497 oysters from Moreton Banks in March and April 1955 (Table 2). During these months there is a general ripening of the gonad of the same order as that observed in Torres Strait, the indication being that a major spawning is imminent.

TABLE 3

SEASONAL DENSITY OF SPAT SETTLEMENT AS INDICATED BY THE NUMBERS SETTING ON SPAT PLATES AT POSSESSION ISLAND

Period of Exposure	Average Monthly Density, *fucata* Spat	
	Identified	Estimated
13. vi.53–13. ix.53	4	29
13. ix.53–14. xii.53	17	27
14. xii.53– 8. iii.54	0	1
8. iii.54–24. v.54	10	15
24. v.54–14.viii.54	30	64
14.viii.54–15. xii.54	2	2
15. xii.54–17. iii.55	47	50
17. iii.55–22. vi.55	5	5
22. vi.55–22.viii.55	15	25
22.viii.55–18. xi.55	21	26
18. xi.55–22. iii.56	5	6

(ii) *Seasonal Spatting Intensity.*—Records have been kept by J. S. Hynd of the seasonal density of spat settlement on artificial collectors of standard area. Since recently settled spat of *P. fucata* (less than 1 cm dorsoventral measurement) are difficult to distinguish from those of *P. albina*, the total catch of either species must be estimated. Estimates are based on the relative frequencies of larger (identifiable) spat of the two species during adjacent periods (see Tranter 1958*c*), and are very approximate. The actual numbers identified, and the estimated totals, are given in Table 3 in terms of mean monthly values. It would appear from this evidence that spat settlement is practically continuous, with irregular periods of greater spatting intensity; however, since the observational periods are broad ($2\frac{1}{2}$–4 months), the continuity of settlement may be more apparent than real. The periods of greatest spatting intensity were May–August 1954 and December 1954–March 1955, which appear to be related to the major spawnings of May–June 1954 and February 1955 (see Fig. 2). It is more difficult to interpret the occasional relatively high intensity of spatting during other periods.

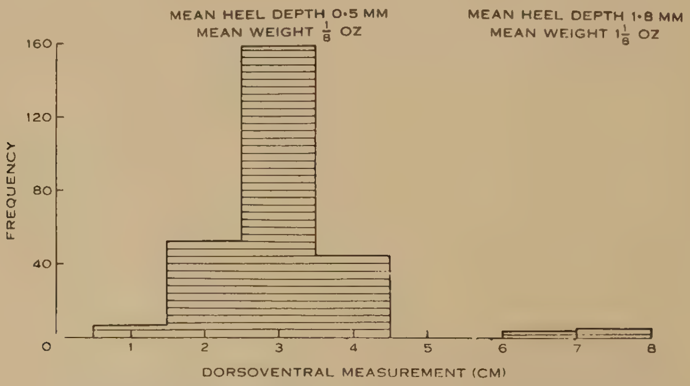

Fig. 3.—Length frequency distribution of the total *P. fucata* catch from the hull of M.V. *Reliance*, October 1, 1953 (last cleaned, July 1952).

On one occasion, a particular catch indicated that there had been a recent spatfall. This was the M.V. *Reliance* material of October 1, 1953 (Fig. 3), the greater part of which had a dorsoventral measurement of 2–4 cm. Heel depth measurements placed the age of this group at 3–4 months; that is, they had arisen from a spawning in May or June.

The spatting evidence, therefore, although of limited significance, supports the conclusions based upon gonad examination.

(*c*) *Age at First Maturity*

Represented in histogram form in Figure 4 are the percentage frequencies of stage 0 (empty) gonads per class interval of heel depth, based on observations made during the period December–May. At this time, gonads in the seasonally undifferentiated state are at a minimum; such being the case, the frequencies of stage 0 gonads, as shown in the histogram, may be regarded as a close approximation to the frequencies of *immature* gonads, and the point at which there is a sudden decrease to a permanently low level, as the stage at which the species reaches sexual maturity. This occurs between 0·5 and 1·0 mm of heel depth, at which stage oysters are approximately $3\frac{1}{2}$–7 months old.

Since there are often two major spawnings a year, it is possible that an individual may spawn twice in its first year. Other evidence supports this: the Banda Rock buoy material of October 19, 1955, was sectioned and examined histologically for germ cell development. By this time, a number of gonads had begun to differentiate, the percentage decreasing with size since the group was less than 12 months old. Table 4 shows that over 50 per cent. of those with a dorsoventral measurement of 2·6–3·0 cm (heel depth less than 0·5 mm) had already matured, or were preparing to do so the following summer. Growth rate measurements of buoy material (Table 1), and the length frequency distribution of the present sample (Fig. 5), indicate that such a group would be 2–3 months old; it would therefore have arisen from the autumn spawning. It is conceivable that this group could spawn both in January and again the following autumn, in which case there would be two spawnings within the first 12 months.

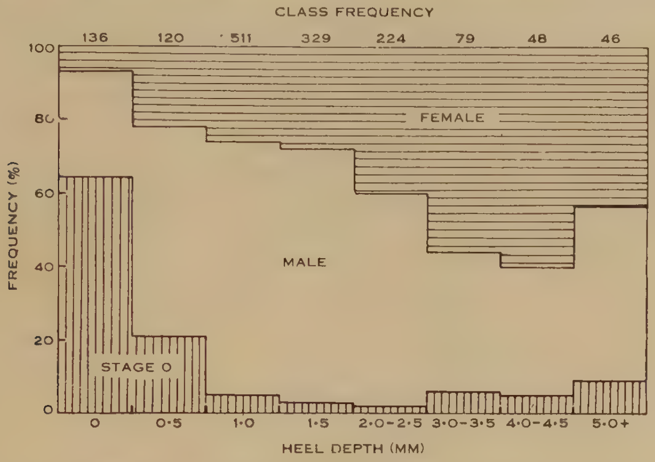

Fig. 4.—Histogram showing the percentage frequency of male, female, and stage 0 (undeveloped) gonads in the various size (heel depth) groups of the Australian *P. fucata* population; material principally from Torres Strait and Moreton Bay.

TABLE 4

HISTOLOGICAL GONAD STATE OF MATERIAL FROM BANDA ROCK BUOY, OCTOBER 19, 1955

The percentage values indicate the frequency of individuals whose gonads have matured or are preparing to do so over the next few months

Dorsoventral Measurement (cm)	2·1–2·5	2·6–3·0	3·0–4·0	4·0–5·0	5·0+
Gonad differentiation frequency (%)	7	58	63	71	77
Class frequency	14	12	16	21	13

(*d*) *Sex Ratio and Sex-Change*

Attention has already been drawn to Figure 4, in which a continual decrease in the proportion of immature gonads over the heel depth range 0·5–1·0 mm signifies sexual maturity. Shown also are the increasing proportions of males and females.

After sexual maturity, there is a significant increase (28 per cent.) in the female fraction at the expense of the male fraction. Such instability is characteristic also of *P. albina* (Tranter 1958*c*) and *P. margaritifera* (Tranter 1958*d*). The phenomenon has previously been discussed in full, and only two explanations are feasible: change of sex and differential mortality. While there is no evidence in this species that young males are less viable than young females, evidence which will shortly be presented shows that sex-change does take place.

In view of this, it may be questioned whether the first-year increase in the proportion of females (Fig. 4) is really associated with the attainment of sexual maturity, with protandric sex-change which is masked by the attainment of sexual maturity, or with a combination of these two factors.

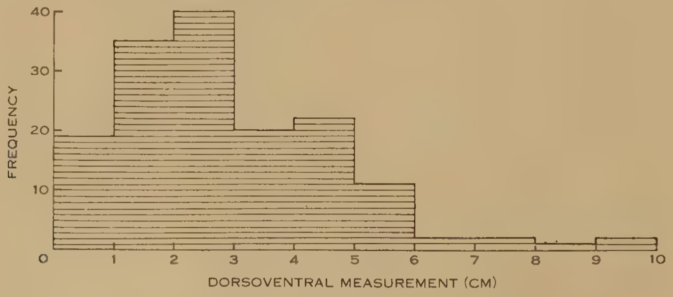

Fig. 5.—Length frequency distribution of oysters from Banda Rock buoy, October 19, 1955; period of exposure 12 months.

The recorded evidence of sex-change is as follows: a number of oysters less than 2 years old were sexed and tagged, and their gonads examined at intervals. In addition to the protandric sex-change which might have been expected on the face of the evidence already presented, protogynic sex-changes were also recorded (Table 5). The significance of this has been discussed earlier (Tranter 1958*c*). Briefly, this means that, if protogynic changes are normal in nature, then the frequency of protandric change is greater than is indicated by the increasing proportion of females shown in Figure 4.

V. Continuous Observations on the Reproductive History of a Particular Spat Group (the Possession Island Material)

(*a*) *Origin*

On November 19, 1955, two surface collectors were placed beneath the Possession Island raft by J. S. Hynd to collect the spat of *P. maxima*. When the first collector was raised on March 10, 1956, large numbers of *P. fucata* were found to have settled. Although only a few live specimens were obtained, it was realized that here was an opportunity to follow the early reproductive history of the species with material of known age. Accordingly, the catch from the second collector, raised on August 4, 1956, was landed alive at the laboratory.

There had been very little spat settlement over the intervening period (see Fig. 6). Therefore the catches from both collectors originated from the same spatfall, and the two sets of observations may be pooled and treated as continuous records of the same spat group. The spatfall in question took place between November 19, 1955, when the collector was laid, and March 10, 1956, when it was raised, a period of 4 months; however, it is possible to place the occurrence of heaviest spat settlement more precisely than this. There would probably have been no settlement in November, since new collectors require approximately a fortnight's conditioning.

TABLE 5
OBSERVED SEX-CHANGES
Material predominantly less than 2 years old

Observational Period	Males		Females	
	Initial No.	No. of Changes	Initial No.	No. of Changes
August–November 1953	45	0	1	0
November 1953–February 1954	45	5	7	1
February 1954–April 1955	25	0	6	4

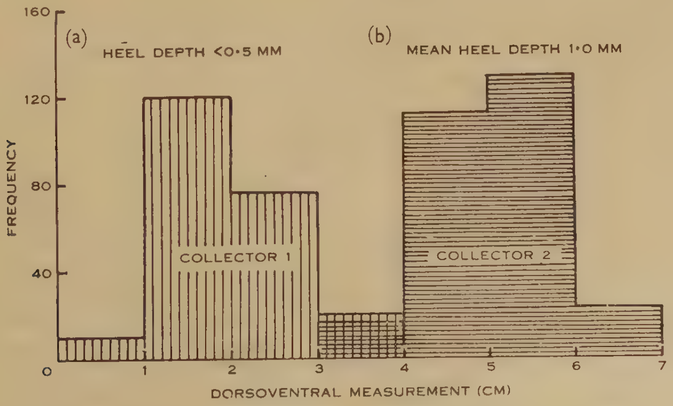

Fig. 6.—Length frequency distribution of *P. fucata* catch on Possession I. collectors: (*a*) Collector 1: laid 19.xi.55, taken up 10.iii.56; 231 specimens; (*b*) Collector 2: laid 19.xi.55, taken up 4.viii.56; 280 specimens.

Since spawning takes place to some extent over the whole of the December–March period, it can be assumed that, of the total catch (231 specimens), the first would have settled in December and the last in March. It is known that the growth rate in the dorsoventral dimension varies with the individual; nevertheless it is considered that, at this early stage and under these (uncrowded) conditions, the largest may be regarded as the first to have settled, and the smallest as the last to have settled. The length frequency distribution of the catch (Fig. 6(*a*)) is therefore an indication of spat settlement intensity over the December–March period. This is positively skewed toward dorsoventral measurement frequencies of 1–2 cm, and if the above assumptions are correct, this means that the greatest intensity of spat settlement occurred in February and to a lesser extent in January. Wada (personal communication) says the larval period is 2–3 weeks. Therefore the major part of the catch would have had their larval origin in January. This is regarded in the following discussion as the date of origin of the group as a whole, though it is conceded that, for any one specimen, this may be in error to the extent of a month either way.

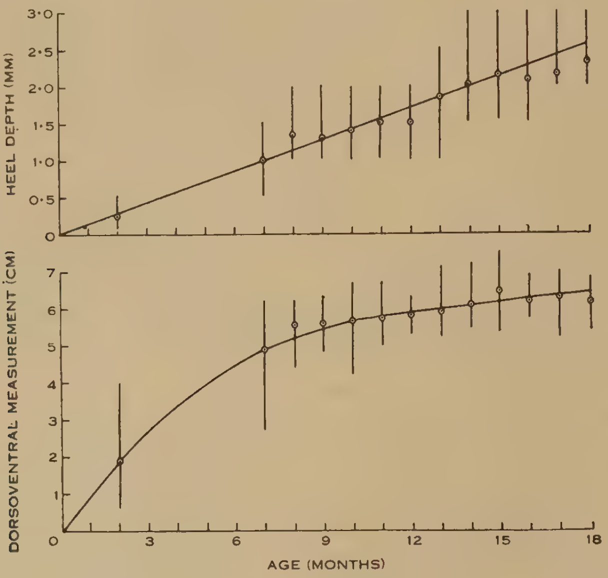

Fig. 7.—Early growth rate of *P. fucata*; based on continuous observations upon the Possession I. spat group (larval origin: January 1956). The values at 2 months represent the mean growth of 231 spat from one collector as at March 10, 1956; the values at 7 months represent the mean growth of 280 spat from another, adjacent, collector as at August 4, 1956; subsequent values are the means of monthly samples of 20 from the latter group. The vertical lines through each mean indicate the range of values within each sample. The curves represent the mean rate of growth of the group over the first 18 months. Heel depth measurements are to the nearest half millimetre.

(*b*) *Rate of Growth*

Assuming that the spat group had their origin in January 1956, records are available of their growth at 2 months (March 10), 7 months (August 4), and at monthly intervals for the next year. The mean values at each examination are plotted in Figure 7, and the range within any one sample is indicated by a vertical line through each mean.

Since heel depths are measured to the nearest half millimetre, the class interval adopted has been relatively coarse. This has meant that heel depth increase is shown to be less gradual than is actually the case. Nevertheless the relationship with age is approximately linear; on the average, increments are a little less than a millimetre every 6 months for the first 18 months of life.

On the other hand, the curve of dorsoventral measurement against age is exponential. This may be due partly to a slowing-up of growth in the dorsoventral dimension when the catch was transferred to Thursday Island.

(*c*) *Development of the Gonad*

The first observations on living material were made on ten of the largest spat from the first collector. In three of these, the gonad was already visible. The fine network of primary follicles could be seen radiating from the genital pore region as in *P. albina* (Tranter 1958*a*, Plate 2, Fig. 1). When these were sectioned, germ cell differentiation was found to be well advanced. Two were male, and contained fully developed spermatozoa at the Md_3 stage (see Tranter 1958*d*); the other, surprisingly, was female (Fd_2). Sections of the remainder showed that, although follicles were not visible macroscopically, the gonad had already begun to develop. In two of these, there was no germ cell differentiation; the primary follicles were minute (less than 30 μ in diameter) and consisted merely of cords of stem cells. In the others, germ cell differentiation (male) was in progress but gametes had not yet been formed. It seems fairly certain, then, that gamete formation marks the stage in gonad differentiation at which follicles become visible macroscopically.

Since the above specimens were amongst the largest from the first collector, it may be assumed that they were approximately 3 months old at examination (March 15), and represent the stage of gonad differentiation reached by the majority in late March or April. If this rate of development were maintained till, say, the end of May, one would expect the whole group, by this time, to have reached maturity and possibly some to have spawned.

That spawning did take place in a number of cases is indicated by the histological gonad condition of the August sample (Table 6): 30 per cent. of the gonads contained residual gametes; in the 60 per cent. which were inactive, the follicular system was well established (although few germ cells were present) and occasional phagocytes were to be seen within the follicles.

The evidence therefore suggests that the Possession Island spat group, which was derived from a midsummer spawning, reached sexual maturity the following autumn, at an age of 4–5 months.

The histological gonad condition of the group during the following year, as shown by regular monthly samples of 20, is given in Table 6. In general, August–September was a period of recovery and inactivity; the gonads of half the group were inactive, and in others residual gonad products were being resorbed. During September, in a few instances, gonia were being laid down, and in an occasional specimen meiosis had been initiated.

During October, gonad activity prevailed, and by November all gonads were ripe or nearly so. Gonad ripening continued into December when a few individuals

TABLE 6

HISTOLOGICAL GONAD CONDITION OF THE POSSESSION ISLAND SPAT GROUP FROM THE AGE OF 7 TO 19 MONTHS

Date	1956					1957							
	20.viii.	17.ix.	15.x.	15.xi.	17.xii.	18.i.	21.ii.	25.iii.	23.iv.	20.v.	18.vi.	15.vii.	13.viii.
Histological Diagnosis	Md_1	Md_1	Md_1	Md_4	Md_4	Md_4	Md_3	Fd_3Mr_2*	Md_2Mr_3	Fd_1	Mr_1	Md_1	Fd_1
	Fd_4	Md_1	Md_1	Md_4	Md_4	Md_4	Md_3	Md_4	Md_4	Mr_1	Mr_1	Mr_1	Mr_1
	Mr_2	Fd_1	Md_1	Md_4	Md_4	Md_4	Md_4	Md_4	Md_4	Mr_1	Mr_1	Mr_2	Mr_1
	Mr_2	Fd_1	Md_1	Md_4	Md_4	Md_4	Fd_4	Md_4	Md_4	Mr_1	Mr_2	Mr_2	Mr_2
	Mr_3	Md_1Mr_3	Md_2	Md_4	Md_5	Md_4	Md_5	Md_4	Md_4	Fr_1	Fr_2	Mr_2	Mr_2
	Mr_3	Md_2	Md_2	Md_4	Md_5	Md_4	Md_5	Md_4	Md_4	Mr_2	Fr_2	Mr_2	Mr_3
	Mr_3	Md_2	Md_2	Md_4	Md_5	Md_4	Fd_5	Md_4	Md_5	Mr_2	Mr_3	Mr_2	Mr_3
	Mr_3	Md_3	Md_2	Md_4	Md_5	Md_5	Fd_5	Md_4	Md_5	Mr_2	Mr_3	Mr_2	Mr_3
	i	Mr_2	Md_2	Fd_4	Md_5	Fd_5	Mr_1	Md_4	Fd_5	Mr_2	Mr_3	Mr_3	Mr_3
	i	Mr_3	Md_2	Fd_4	Md_5	Mr_1	Mr_1	Fd_4	Mr_1	Mr_2	Mr_3	Mr_3	Mr_3
	i	i	Md_2	Fd_4	Md_5	Mr_1	Mr_2	Fd_4	Mr_1	Mr_2	Mr_3	Mr_3	Mr_3
	i	i	Md_3	Md_5	Md_5	Mr_1	Mr_2	Fd_4	Mr_1	Mr_3	Mr_3	Mr_3	Mr_3
	i	i	Md_3	Md_5	Fd_5	Mr_1	Mr_2	Md_5	Fr_1	Mr_3	i	Fr_3	i
	i	i	Md_3	Md_5	Fd_5	Mr_1	Mr_3	Fd_5	Fr_1	Mr_3	i	i	i
	i	i	Md_3	Md_5	Fd_5	Mr_1	Mr_3	Fd_5	Mr_2	Mr_3	i	i	i
	i	i	Md_3	Md_5	Mr_1	Fr_1	Fr_3	Mr_1	Fr_2	Mr_3	i	i	i
	i	i	Fd_3	Md_5	Mr_1	Fr_1	Fr_3	Mr_1	Fr_2	Fr_3	i	i	i
	i	i	Md_4	Md_5	Mr_1	Fr_1	i	Mr_1	Fr_3	Fr_3	i	i	i
	i	i	Md_4	Mr_1	Fr_1	Mr_2	i	Mr_1	Fr_3	Fr_3	i	i	i
	i	i	Fd_4	Mr_1	Fr_1	Mr_2	i	Fr_1	i	i	i	i	i
Total†	5 : 16 : 12	12 : 8 : 10	48 : 0 : 0	79 : 2 : 0	71 : 5 : 0	38 : 13 : 0	34 : 20 : 3	62 : 7 : 0	37 : 20 : 1	1 : 40 : 1	0 : 27 : 8	1 : 28 : 7	1 : 27 : 8
Percentage Index†	5 : 27 : 60	12 : 13 : 50	48 : 0 : 0	79 : 3 : 0	71 : 8 : 0	38 : 22 : 0	34 : 33 : 15	62 : 12 : 0	37 : 33 : 5	1 : 67 : 5	0 : 45 : 40	1 : 47 : 35	1 : 45 : 40

* Bisexual gonad.

† Development : regression : inactivity.

began to spawn. Spawning gathered momentum during late December, and by January more than half the group were involved. By February these had spawned more or less completely and occasional gonads had regressed to a state of undifferentiated inactivity similar to that prevalent during the previous August and September.

March was a period of gonad re-ripening. This process was extremely rapid since, in most cases, germ cell development took place within the same follicles which had been laid down previously and had not yet regressed to any great extent (Plate 1, Fig. 3). The two phases of gonad development may therefore be regarded as part of the one continuous breeding season.

In April, a major spawning commenced, which, in May, involved the whole group. Many oysters spawned only partially during this period (Plate 1, Fig. 5) and their gonads emptied gradually over the succeeding months, principally by phagocytic resorption; although some extrusion of residual products may have taken place, it is considered that these would have been, in the main, inviable. Gonads which spawned completely during April and May quickly regressed to a state of undifferentiated inactivity which persisted over the next few months. The months of June, July, and August, therefore, constitute a period of gonad recovery, as did August and September of the preceding year. It is evident, then, that the period June–September represents a "wintering phase" in the annual breeding cycle.

The major trends described above are represented graphically in Figures 8(*a*) (macroscopic observation) and 8(*b*) (histological observation). The latter curves are derived from the tabulated list of histological stages (Table 6) in the same way as for *P. albina* (Tranter 1958*c*) and *P. margaritifera* (Tranter 1958*d*). In brief, the plotted points represent the general extent of gonad development and gonad regression in each sample relative to that in which every gonad in the sample is, respectively, either fully ripe (d_5) or in the last stages of regression (r_3); in like manner, the curve of gonad inactivity represents the percentage frequency of inactive gonads (i).

Summarizing, observations on the gonad condition of this group over the period August 1956–August 1957 indicate a definite pattern of seasonal breeding behaviour. The annual cycle consists of a wintering period, June–September, and a period of gonad activity, October–May. The latter may be regarded, broadly, as the breeding season. A certain amount of spawning occurs throughout this period, but there are two maxima: January–February and April–May.

(*d*) *Sex Ratio and Sex-Change*

The numbers of each sex in the monthly samples are listed in Table 6. If those samples are omitted which contain large numbers of inactive gonads, the remainder give some indication of the sex ratio of the group as a whole at the time of sampling. These are shown in Table 7 in conjunction with the age of each sample. There is a trend toward a lower sex ratio—that is, toward more and more females—which suggests that protandric sex-changes have taken place within the group.

One specimen from the March (1957) sample is proof of this. The gonad, classified Fd_3Mr_2, was bisexual. At this time, there was rapid re-ripening of gonads following the major spawning in January. In this specimen the male spawning was either late or prolonged, and the vigorous differentiation of the female phase somewhat premature. Consequently the two phases overlapped, and the bisexual condition resulted. Had examination of the gonad been a few weeks earlier or later, possibly no bisexuality would have been evident; therefore, unless sampling is at shorter intervals, the bisexual condition may be missed completely.

Amongst the ten specimens examined in March 1956 (ages less than 4 months), there was one female. It cannot, then, be doubted that occasional individuals mature directly as females.

TABLE 7

VARIATIONS IN SEX RATIO OF THE MONTHLY SAMPLES FROM THE POSSESSION I. SPAT GROUP

Data from Table 6. Samples containing a high percentage of inactive gonads have been omitted

Date	Age of Sample (Months)	No. of Males	No. of Females	Sex Ratio (Males/Females)
October 1956	9	18	2	9·0
November 1956	10	17	3	5·7
December 1956	11	15	5	3·0
January 1957	12	16	4	4·0
February 1957	13	12	5	2·4
March 1957	14	13	7*	1·9
April 1957	15	12	7	1·7
May 1957	16	14	5	2·8

* One specimen changing from male to female: Fd_3Mr_2.

VI. COMPARISON OF DATA

The oysters of the Possession Island spat group, dealt with in the preceding section, were approximately the same age and, subsequent to spat settlement, were subject to the same environmental conditions. The behaviour of such a group, compared with that of samples from the heterogeneous natural population, is therefore of significance in the interpretation of the data as a whole. The conclusions are reviewed below.

The dorsoventral measurement growth curve for the Possession Island material is of an exponential nature (Fig. 7); that is, the rate of increase is greatest early in life. This agrees with the fact that specimens from buoys grew to maximum size (9·0–9·7 cm) within 12 months (Table 1). Since the mean dorsoventral measurement of the Possession Island material at 12 months was only 6·7 cm, one can conclude that the conditions for growth afforded this group were less favourable than those provided by the buoy environment.

Both sets of data show that the heel depth : age relationship is approximately linear, thus supporting the validity of the heel depth method of age determination (see Section IV(*a*)). The fastest-growing specimens from the buoys grew to a heel depth of 2·0 mm in less than a year; in the Possession Island samples, the first 2·0 mm recorded was at 8 months and the first 2·5 mm at 13 months (Fig. 7). These (fastest) rates of growth are very similar. The *mean* rate of growth in this dimension is somewhat less; in the Possession Island material it is of the order of 1·7 mm for the first 12 months (see straight line through plotted means); tagged specimens reached a heel depth of 5 mm in 3 years (Fig. 1). Thus the mean rates of increase shown by the Possession Island material and by tagged specimens also are similar.

Observations on gonad development in the general population lead one to conclude that the species reaches sexual maturity at the age of $3\frac{1}{2}$–7 months (Fig. 4). In the Possession Island material, gonad differentiation was observed at 3 months, and it was concluded that sexual maturity would have been reached in approximately 5 months. Whether this did happen is not certain, but the fact that gonads were observed with residual products in August is highly suggestive. To this extent, then, the two groups of data are in agreement.

With respect to sex-change, Figure 4, which is based on all available observations, shows a trend toward a higher percentage of females amongst older oysters: at first maturity, there are approximately three males to every one female; in the second year, the ratio is of the order of 1·5 : 1; in the third year, females predominate. A comparable trend has been shown to occur, also, when the observations are upon a particular group (Table 7). At 9 months, the ratio of males to females in the Possession Island group was of the order 9 : 1; at 12 months, 4 : 1; and in the first few months of the second year, 2 : 1. Such a trend is the result of protandric sex-change as is illustrated by the bisexual gonad in the March (1956) sample of the Possession Island material; here, at 14 months, the sex was changing from male to female. That protogynic sex-changes also occur is shown by the observations on tagged material; that none were recorded among the Possession Island samples is not surprising, since there were few females to start with.

Thus the species is hermaphrodite as are *P. albina* and *P. margaritifera*. Although a case was observed where the sex at first maturity was female, this is interpreted to mean that protandry is not a universal feature, and not that occasional specimens are dioecious.

Concerning the breeding season of the species, observations on the gonad condition of regular samples from the general Torres Strait population (Fig. 2) show that the most consistent feature is the occurrence of an autumn spawning, preceded on occasions by one of comparable intensity in mid or late summer; on these grounds, the period midsummer to autumn was given as the spawning season. Such a breeding pattern is shown also by the Possession Island material (Fig. 8); however, gonad sections reveal that a few individuals spawn as early as November; therefore the period November–May is essentially one continuous breeding season, in which there are two maxima of spawning intensity.

Both groups of data show that there is a well-marked wintering period, and that seasonal gonad development invariably begins in spring. Nevertheless there is often restricted gonad activity during winter (1953), and a brief phase of gonad inactivity after the summer spawning (as in early 1953 and 1957). This explains to some extent why spat settlement appears to be practically continuous (see Table 3).

It is now evident that the two groups of data are substantially in agreement.

VII. Discussion

It is well known (Pearson, Malpas, and Kerkham 1929) that, in Ceylon, *P. fucata* becomes sexually mature in the first year; Hornell (1905) had, in fact, observed well-developed gonads in individuals of 3½ months. This agrees with the present observations. There is no published information dealing with sexual maturity of the species in Japan.

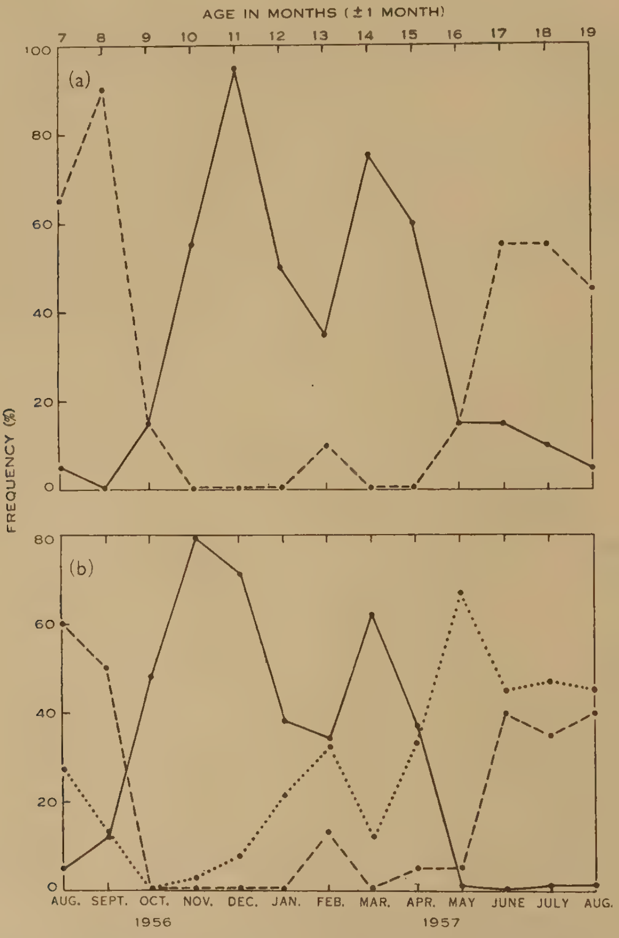

Fig. 8.—Development history of the gonad in the Possession I. spat group. (*a*) Macroscopic observation; (*b*) histological observation. ———, development; – – – –, inactivity; . . . . . ., regression.

The variability of the sex ratio among different groups of material had been noted by earlier workers; however, with the exception of Hynd (C.S.I.R.O. Aust. 1951) who noted protandry in both *P. fucata* and *P. albina*, there was no attempt to correlate such variation with sex-change. Although Herdman and Hornell

(1906), in Ceylon, found little variation in the sex ratio from 87 males : 71 females, Kelaart (1857) had found in the same area only three to four males per hundred and had assumed this to be normal. It is now apparent that he was dealing with an older population, whereas the data of Herdman and Hornell were recorded soon after a series of heavy spatfalls had initiated a new pearlfishery (Hornell 1916; Pearson, Malpas, and Kerkham 1929). In later years, as spatting failed on the Ceylon beds, Hornell himself (Boutan 1925) found a preponderance of females similar to that encountered by Kelaart. It has been shown also (Wada and Wada 1939) that sex-change is prevalent in 2–4 year old Japanese populations; of 54 males examined in 1936, 22 had changed to female by 1937; protogynic changes were also recorded. These various observations show that the species is sexually unstable.

Herdman and Hornell (1906) believed *P. fucata* to be "permanently dioecious", and gave the following reasons:

(1) Herdman observed a preponderance of males in February and March, and Hornell encountered the same disproportion at other times of the year. It was apparently expected that sex-change would result in a seasonal variation in the sex ratio.

(2) An experiment had shown that the sex of four specimens (three of which were male) had not changed between one spawning and the next.

(3) Gonad dissection failed to disclose any bisexuality.

(4) Histological observations confirmed this.

It can be shown that these workers made certain assumptions which are not justified. In the first place, it does not necessarily follow that sex-change will result in seasonal variation of sex ratio. This presupposes that changes of sex will occur in the population more or less concurrently. Even if this were so, the resultant seasonal increase in the percentage of females would be offset, in a protandric species, by a seasonal increase in the percentage of young males, as spat reached sexual maturity, not to mention any protogynic change which might take place, or the decrease in the number of older (predominantly female) oysters due to selective fishing.

Their second argument is based upon very limited evidence; all that can be inferred from their observations is that change of sex does not invariably take place after every spawning.

Concerning the detection of bisexuality by dissection, it should be pointed out that this is often difficult, unless the overlapping of phases is so great that there are present, within the follicles, functional gametes of both sexes; when one phase is in the early stages of differentiation, the developing germ cells tend to remain attached to the follicle wall, and do not readily show up in a smear.

Although Herdman and Hornell failed to find any sign of bisexuality in gonad sections, Ojima and Maeki (1955) noticed several instances of this amongst a sample of 30 oysters from the Japanese population; we have already seen that there was one such case in the Possession Island material, and many more were indicated

(Table 7). The fact that these are so rarely encountered in sectioned material, compared with the frequency which is indicated by the variation in sex ratio is, in the present author's opinion, due to the following factors:

1. The material sectioned may not be at the age when sex-changes occur most frequently.
2. The change occurs with such rapidity that the bisexual condition is only transient.

It might be expected that sex-change occurs when the gonad is in the indifferent resting condition. However, this does not appear to be the case: changes recorded by the author (Table 5) occurred between November and April when the gonad is usually active. The bisexual gonad noted in the Possession Island material in March came from a sample in which there was vigorous gametogenic activity; Ojima and Maeki obtained their material during May and June when (in Japan) gonads are ripening rapidly. There is no exact indication when the changes observed by Wada and Wada took place.

The breeding season of *P. fucata* in Ceylon waters has received a great deal of attention. Herdman and Hornell (1906) believed that the species breeds to some extent throughout the year, with spawning maxima in midsummer (May–July) and midwinter (November–January). Malpas (1933) agreed with this.

The breeding cycle of the species in Australia resembles that in Ceylon, in that there are two spawning maxima each year; but, whereas in Ceylon there are two separate breeding seasons, in Torres Strait the two spawning maxima form part of the one attenuated breeding season embracing all but the coldest months of the year.

In Ceylon (Malpas 1933) spawning is stimulated by the ingress of low salinity water resulting from the seasonal rains of the south-west monsoon (summer) and north-east monsoon (winter). In Japan (Craig, unpublished data), spawning activity becomes intense during the height of the spring tides in the latter part of July and early August, when the oyster beds are subjected to high sea temperatures. Spawning, in Australian waters, is not dependent on an influx of low salinity water as it is in Ceylon, and it is not possible from the data available to see a correlation with any other environmental factor.

It is interesting to compare the reproductive biology of this species with that of *P. albina* and *P. margaritifera*. *P. fucata* and *P. albina* have the following features in common.

1. Sexual maturity is reached within 6 months.
2. A major spawning occurs in "autumn".
3. Spawning is frequently only partial, and there is extensive phagocytosis of unspent gonad products.

Features common to *P. fucata* and *P. margaritifera* are:

1. A moderately restricted breeding season.
2. A tendency toward biannual spawning maxima.
3. A higher percentage of females at first maturity than *P. albina*.

Of the features which are common to all three species, perhaps the most significant are the following:

(1) The pattern of gametogenesis.

(2) They are protandric hermaphrodites.

(3) Both protandric and protogynic sex-changes occur.

(4) The primary oocyte becomes activated immediately before or during spawning.

(5) The egg is fertilized at the metaphase stage of the first reduction division.

It is possible that these features will be found to be characteristic also of other species in the genus.

VIII. ACKNOWLEDGMENTS

The author is indebted to Mr. Garth Lahey of the Government Analyst's Department, Brisbane, for carrying out chemical analyses on the white layer structure, and to Dr. W. B. Mather for sudan black preparations of the same material. Mr. J. S. Hynd made available the catch from the Possession Island collectors and the counts from spat plates. The Commonwealth Navigation and Lighthouse Service is again to be thanked for permission to secure material from light-buoys after cleaning and the Queensland Harbours and Marine Department for providing transport to the pearl oyster beds of Moreton Bay. The investigation was carried out, in part, at the Thursday Island Field Station provided by the Queensland Government and maintained by C.S.I.R.O.

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EXPLANATION OF PLATE 1

bb, tissue staining heavily with Bismarck brown; *ct*, connective tissue; *m*, metaphase configuration; *N*, nucleus; *n*, nucleolus; *ooc r*, residual oocytes; *pb*, polar bodies; *s*, mantle surface; *spc I*, primary spermatocyte; *spc II*, secondary spermatocyte; *spg*, spermatogonia; *spz*, spermatozoa.

Fig. 1.—A ripe unactivated oocyte, showing the large conspicuous nucleus (germinal vesicle). Phase contrast. × 700.

Fig. 2.—The ovary immediately prior to spawning showing the oocytes after activation. The nucleus has broken down and the chromosomes are in the metaphase of the first reduction division. × 280.

Fig. 3.—Male follicles in which active spermatogenesis has recommenced before the cells of the preceding phase (*spz*) have completely disappeared (March 1957). × 70.

Fig. 4.—Section across the white glandular "mucoprotein layer" covering the gonad, showing the heavy staining with Bismarck brown, × 70.

Fig. 5.—A residual ovary (July 1957). × 70.

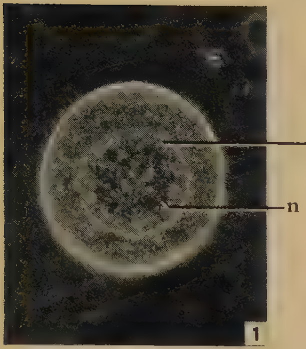
Fig. 6.—Section across the wall of a male follicle showing primary spermatocytes in late diplotene, × 700.

Fig. 7.—Primary spermatocytes (pachytene and early diplotene) and secondary spermatocytes—for comparison. × 700.

Fig. 8.—Spermatogonial metaphase showing the diploid chromosome complement. × 1400.

Fig. 9.—The haploid chromosomes of the fertilized egg immediately after the second maturation division. × 1050.

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. V



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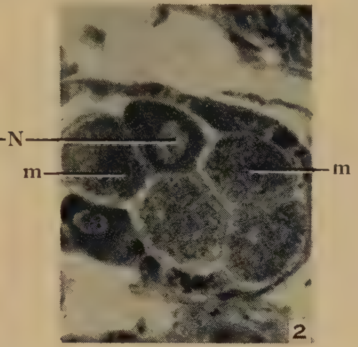

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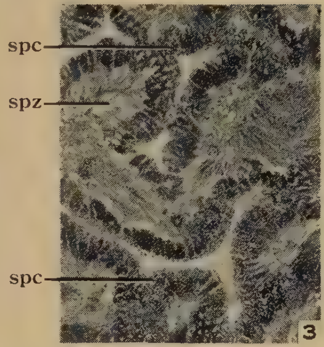

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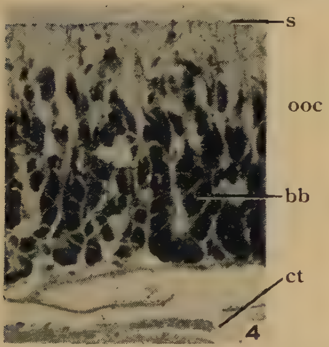

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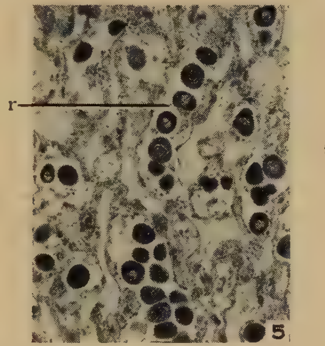

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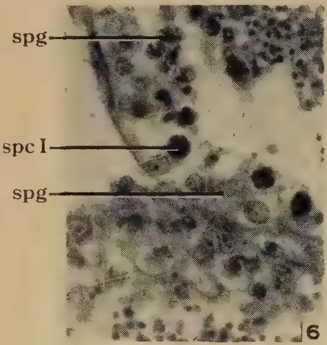
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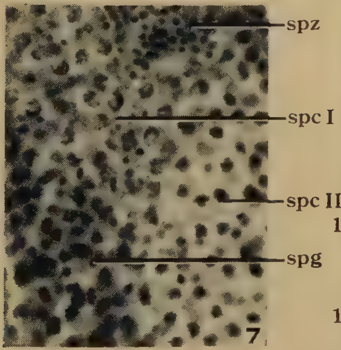
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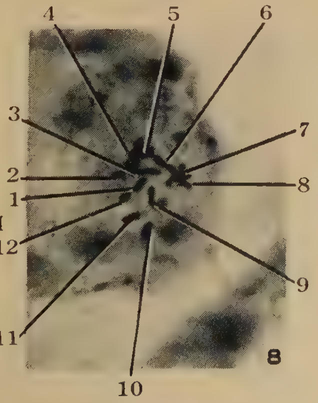
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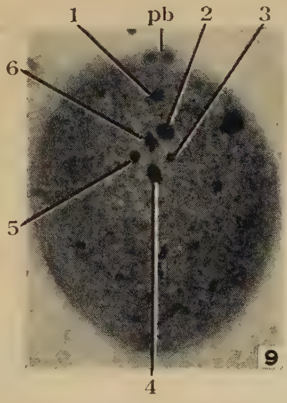

9

THE DISTRIBUTION OF INTERTIDAL CRABS IN THE BRISBANE RIVER

By Barbara Snelling*

[*Manuscript received October* 28, 1958]

Summary

This paper records investigations made on the ecology of intertidal crabs of the Brisbane River.

Traverses were made at selected localities extending from the river mouth upstream to points beyond the limit of tidal influence. Twenty-three species of crabs were found, two of which extend 37 miles upstream. The population was found to fall into four clearly defined vertical zones: (1) sesarmine zone, H.W.N. upwards, (2) ocypodine zone, H.W.N. to M.S.L., (3) upper macrophthalmine zone, M.S.L. to L.W.N., and (4) lower macrophthalmine zone, L.W.N. to L.W.S.

After drought, species not usually found in the river were present in the lower reaches. Freshwater flooding caused disappearance of these from the river and reduced the upstream penetration of one species.

Comparisons with work in other parts of the world show that the estuarine crab distribution in the Brisbane River is similar to that in South Africa and Java. It is suggested that salinity is the most important factor controlling the distribution of estuarine crabs.

I. Introduction

In the estuaries of southern Queensland and northern New South Wales, crabs are a noticeable part of the intertidal fauna and many species are found. Casual inspection of the Brisbane River showed that crabs dominated the river banks of the entire estuarine region. Over most of this their densities were of the order 30/m^2. This appears to contrast with the situation in Britain (Percival 1929; Bassindale 1938), and in California (MacGinitie 1935), but to show similarities with Java (Verwey 1930) and South Africa (Day 1951).

The present investigation was undertaken on the Brisbane River fauna to determine:

(1) the number of species present;

(2) their distribution upstream from the mouth;

(3) their vertical distribution at selected localities;

(4) possible variations related to drought and flood conditions.

It was hoped this would provide a basis for comparison with the situation elsewhere within and outside Australia.

II. Methods

Investigations lasted from September 1956 to June 1958 at selected sites (Fig. 1), extending 37 miles upstream, mileages being measured from the Boat Passage. The frequency of visits varied from about once a fortnight to once a month.

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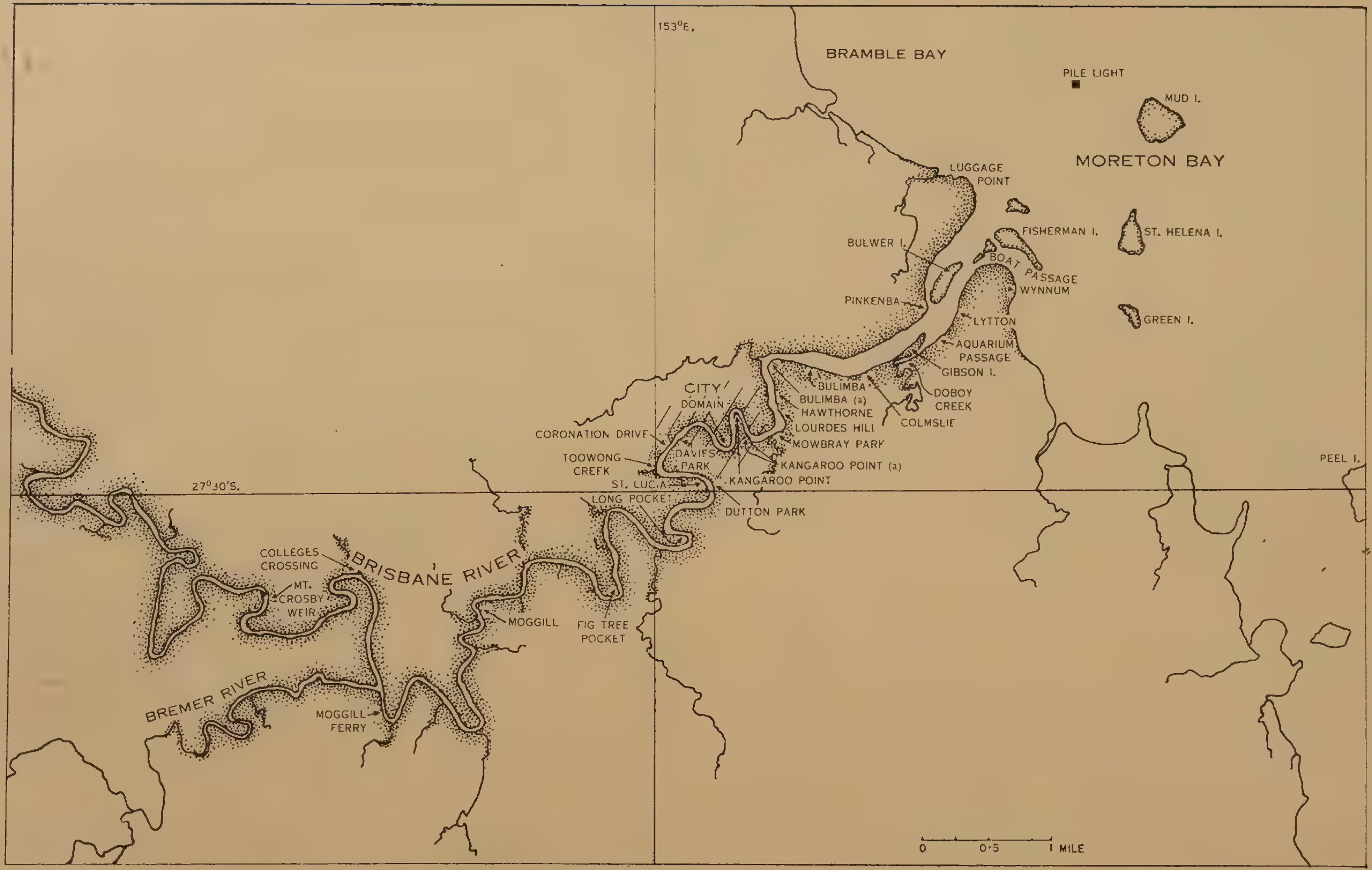
153°E.
BRAMBLE BAY
PILE LIGHT
MUD I.
MORETON BAY
LUGGAGE POINT
FISHERMAN I.
ST. HELENA I.
BULWER I.
BOAT PASSAGE
WYNNUM
PINKENBA
GREEN I.
LYTTON
AQUARIUM PASSAGE
GIBSON I.
CITY
DOMAIN
BULIMBA
BULIMBA (a)
HAWTHORNE
DOBOY CREEK
COLMSLIE
LOURDES HILL
CORONATION DRIVE
MOWBRAY PARK
DAVIES PARK
TOOWONG CREEK
KANGAROO POINT (a)
KANGAROO POINT
ST. LUCIA
PEEL I.
27°30'S.
LONG POCKET
DUTTON PARK
COLLEGES CROSSING
BRISBANE RIVER
MT. CROSBY WEIR
MOGGILL
FIG TREE POCKET
BREMER RIVER
MOGGILL FERRY
0
0·5
1 MILE

Fig. 1.—Map of the Brisbane River showing localities investigated.

At each locality, after samples of all species were collected, a traverse was made in a typical area from well above high water to water level. Adjacent traverses were often made at points deliberately chosen because of unusual features, e.g. rocky outcrops, absence of mangroves, entry of creeks.

By using tidal data for the Pile Light, which is in Moreton Bay 7 miles from the mouth, and data from the Queensland Department of Harbours and Marine for the time lag for tides at several stations in the river, tidal levels were estimated. The following reference levels were used:

Mean high water spring	H.W.S.
Mean high water	M.H.W.
Mean high water neap	H.W.N.
Mean sea-level	M.S.L.
Mean low water neap	L.W.N.
Mean low water	M.L.W.
Mean low water spring	L.W.S.

The greater the distance from the river mouth, the smaller is the area of river bank between tides, i.e. the area of possible habitats for intertidal crabs. There are two reasons for this: (1) beyond about 25 miles the tidal amplitude decreases gradually, i.e. from 8½ ft at St. Lucia to none at Colleges Crossing; (2) the banks become steeper; in the lower reaches where the river is fairly wide and unrestricted in flow, low tide leaves bare up to 30 yd of gently sloping mud, whereas about 30 miles upstream the exposed width is about 5 ft.

The comparative and semiquantitative scheme of estimating abundance as defined by Endean, Kenny, and Stephenson (1956) was used in the present work as follows: (1) Dominant (D); (2) Codominant (CD); (3) Subdominant (SD); (4) Very Common (VC); (5) Common (C) (less than 20 but more than 5 specimens found); (6) Present (P) (no more than 5 specimens found).

III. Species Encountered

Table 1 gives a list of the 23 species of intertidal crabs collected. All identifications, apart from stated exceptions, were either checked by Mr. F. A. McNeill of the Australian Museum, or checked against specimens (often from the same localities) previously identified by him. Only three species, *Macrophthalmus setosus*, *Halicarcinus australis*, and *Thalamita crenata* were not checked by Mr. McNeill, identification being based upon Tesch (1915, 1918) and Stephenson and Hudson (1957) respectively. The *Sesarma* sp. and *Heteropilumnus* sp. are probably new. They await identification, the former by Dr. Isabella Gordon of the British Museum and the latter by Mr. McNeill. Regarding *Cyrtograpsus* (?) spp., Mr. M. W. F. Tweedie of the Raffles Museum, Singapore, states (personal communication): "The series contains two species. One is, I think, conspecific with *Camptandrium paludicola* Rathbun (Danish Exped. to Siam, Brachyura, 1910, p. 326) . . . The other seems to be a species of the same genus . . . probably undescribed. However, the genus to which both these belong is not, I am almost certain, *Camptandrium*. Tesch (Siboga Monog. 39*c*, 1918, p. 68) spotted this and

TABLE 1

LIST OF INTERTIDAL CRABS OF THE BRISBANE RIVER

Species	Ecological Significance	Habitat	Normal Vertical Range	Distribution (Miles Upstream in Brackets)
Family Ocypodidae				
Cleistostoma mcneilli Ward	Dominant	Burrows in soft mud	H.W.N.–M.S.L.	Colmslie (5) to St. Lucia (18)
Cleistostoma wardi Rathbun	Present	Burrows in firm mud	Above H.W.S.	Mouth to Aquarium Passage (2)
Euplax tridentata Rathbun	Dominant	Burrows in soft mud	H.W.N.–M.S.L.	Mouth to St. Lucia (18)
Heloecius cordiformis H. M. Edwards	Dominant	Gritty dryish mud	H.W.S.–M.H.W.	Mouth to St. Lucia (18)
Leipocten sordidulum Kemp	Present	On mud under stones	M.S.L.–L.W.N.	Mouth to Kangaroo Pt. (12)
Macrophthalmus pacificus Dana	Present	Burrows in soft mud	L.W.N.–M.S.L.	Mouth to Bulimba (6½)
M. punctulatus Miers	Present	Burrows in firm mud	H.W.N.–L.W.N.	Mouth to Bulimba (6½)
M. setosus H. M. Edwards	Dominant	Damp soft mud	L.W.N.–L.W.S.	Mouth to Domain (13½)
Uca longidigitum Kingsley	Dominant or Codominant	Burrows in firm mud	M.H.W.–M.S.L.	Mouth to St. Lucia (18)
U. marionis (Desmarest)	Codominant	Burrows in sandy mud	M.H.W.–M.S.L.	Mouth to Aquarium Passage (2)
Family Mictyridae				
Mictyris longicarpus Latreille	Dominant	Sandy mud	H.W.N.–M.S.L.	Mouth to Aquarium Passage (2)
Family Grapsidae				
Helice haswellianus Whitelegge	Dominant	Burrows in mudbank or under stones	Above H.W.S.–L.W.N.	Mouth to Domain (13)
Cyrtograpsus (?) *paludicola* Rathbun	Present	Under stones	M.S.L.–L.W.N.	Mouth to Bulimba (6½)

TABLE 1 (*Continued*)

Species	Ecological Significance	Habitat	Normal Vertical Range	Distribution (Miles Upstream in Brackets)
Family Grapsidae (*continued*)				
Cyrtograpsus (?) sp.	Present	Under stones	H.W.N.–M.S.L.	Mouth to Bulimba (6½)
Metapograpsus messor (Förskål)	Common	Under stones	H.W.N.–M.S.L.	Mouth to Aquarium Passage (2)
Paragrapsus gaimardi H. Edwards	Present	Under stones on mud	M.S.L.–L.W.N.	Mouth to Colmslie (5)
Sesarma erythrodactyla Hess	Codominant	Burrows in mudbank or in crevices	H.W.S.–H.W.N.	Mouth to St. Lucia (18)
Sesarma sp.	Dominant	Burrows in mudbank amongst mangrove roots	H.W.S.–below H.W.N.	Kenmore (20) to Moggill (37)
Family Xanthidae				
Heteropanope glabra Stimpson	Common	Under stones	Above M.S.L.	Mouth to Aquarium Passage (2)
Heteropilumnus sp.	Present during drought only	Under stones	Above M.S.L.	Mouth to Aquarium Passage(2)
Pilumnopeus serratifrons (Kinahan)	Present during drought only	Under stones	Above M.S.L.	Mouth to Aquarium Passage (2)
Family Portunidae				
Thalamita crenata (Latreille)	Present during drought only	Under stones	M.S.L.	Mouth to Aquarium Passage (2)
Family Hymenosomatidae				
Halicarcinus australis (Haswell)	Common	Under stones on gravelly mud	M.S.L.–L.W.N.	Mouth to Moggill (37)

tentatively referred Rathbun's species to *Cyrtograpsus*. . . . Whether the sp. is really a *Cyrtograpsus* I am by no means sure. It is certainly much smaller than normal species of that genus and a direct comparison might well reveal differences of generic status. Your discovery of a second species, also diminutive, strengthens the supposition that a new genus is needed . . ."

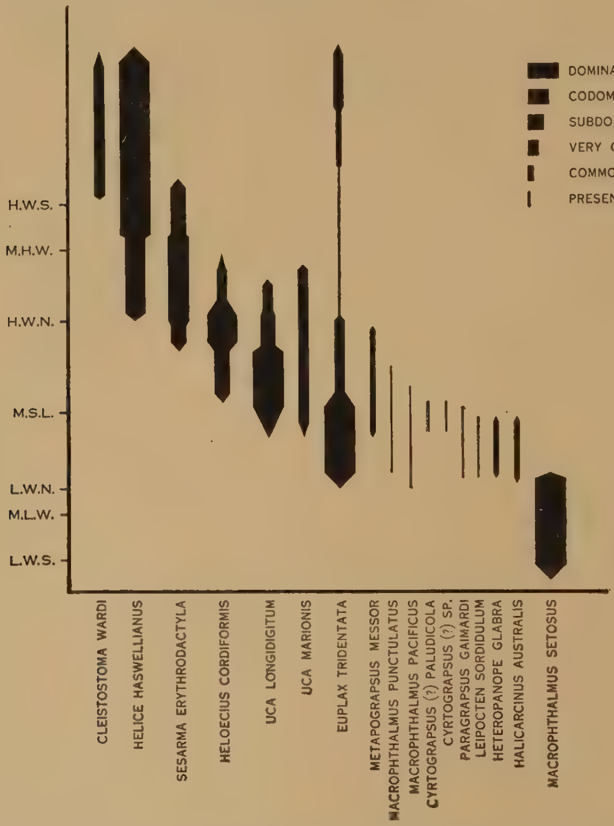

Fig. 2.—Diagrammatic representation of zonation and abundance of crabs at Aquarium Passage.

IV. Habitat Preferences

River crabs may be classified in three main groups according to whether or not they burrow in mud. These are:

Crabs always living in burrows: *Cleistostoma wardi*, *Heloecius cordiformis*, *Macrophthalmus setosus*, *Mictyris longicarpus*, *Sesarma* sp., *Uca longidigitum*, *U. marionis*.

Crabs living under stones if these are present, but otherwise making burrows: *Cleistostoma mcneilli*, *Euplax tridentata*, *Helice haswellianus*, *Macrophthalmus pacificus*, *M. punctulatus*, *Sesarma erythrodactyla*.

Crabs living only under stones: *Cyrtograpsus* (?) *paludicola*, *Cyrtograpsus* (?) sp., *Halicarcinus australis*, *Heteropanope glabra*, *Heteropilumnus* sp., *Leipocten sordidulum*, *Metapograpsus messor*, *Paragrapsus gaimardi*, *Thalamita crenata*, *Pilumnopeus serratifrons*.

V. VERTICAL DISTRIBUTION OF CRABS IN THE BRISBANE RIVER

The question arose early in the work whether the crab population is better divided into horizontal zones or into discrete patches each occupied by a given species or group of species. MacGinitie (1935) preferred not to group fauna into zones but regarded all animals either as individuals or as part of discrete groups.

In the Brisbane River patchiness does occur so that a major area is divisible into several patches of different species (e.g. at Aquarium Passage an area of sandy mud is populated by *Uca longidigitum*, *U. marionis*, and *Mictyris longicarpus*, with the *Uca* species intermingling (Plate 3, Figs. 1 and 2), but *Mictyris* remaining distinct). These groups, however, always occur at comparable heights along the river and it is felt that a significant "zonation of patches" can be recognized. To illustrate this zonation, typical traverses from four localities are given:

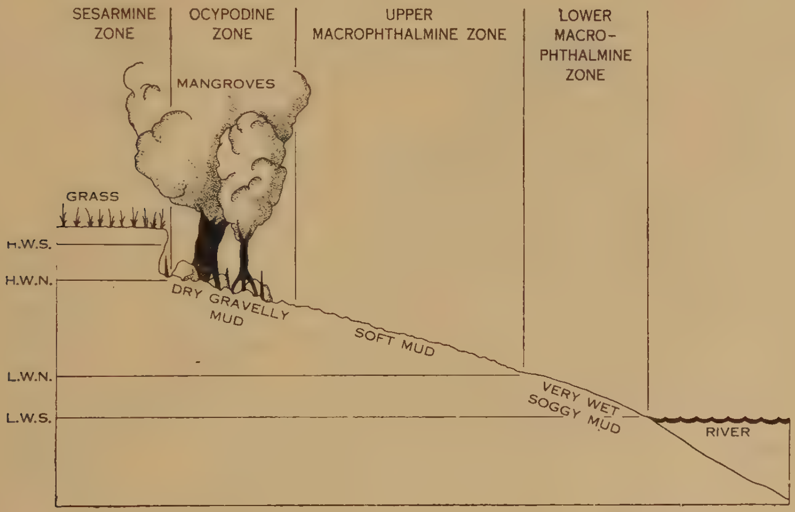

Fig. 3.—Typical profile of river bank based on Bulimba.

(1) *Aquarium Passage*.—Two miles upstream (Fig. 2 and Plate 2, Fig. 1). Above H.W.S. a mudflat stretches for about 30 yd (Plate 1, Fig. 2). Here the only plants are *Salicornia australis* Solander, and *Suaeda* sp. The commonest crab is *Helice haswellianus*, which alone is present where the mud is dry and without puddles. *Cleistostoma wardi* is found where the mud is soft, and *Euplax tridentata* where there are salty pools. From H.W.S. to H.W.N. amongst mangroves, *Sesarma erythrodactyla* occupies the highest situations; *Heloecius cordiformis* is most common where the mud is gravelly, and *Uca longidigitum* is dominant where the mud is damper. *Heloecius* and *Uca* are codominant for most of their ranges. Approaching M.S.L., where the mud is soft and wet, the dominant crab is *Euplax tridentata*. Also in this region, nine additional species are found in small numbers: *Metapograpsus messor*,

Macrophthalmus punctulatus, *M. pacificus*, *Cyrtograpsus* (?) *paludicola*, *Cyrtograpsus* (?) sp., *Paragrapsus gaimardi*, *Leipocten sordidulum*, *Heteropanope glabra*, and *Halicarcinus australis*. These continue to about L.W.N. where they all disappear and *Macrophthalmus setosus* alone is dominant.

(2) *Bulimba.*—Six and a half miles upstream (Figs. 3 and 4). Here the crab distribution is much the same as at Aquarium Passage. *Helice haswellianus* and *Sesarma erythrodactyla* are found above H.W.N. where the mud is hard and stony, and are codominant. (Nearby, where many stones are present, *Helice* is dominant and *Sesarma* subdominant.) From H.W.N. to M.S.L., where the mud is gravelly and firm, *Heloecius cordiformis* and *Uca longidigitum* are codominants. Further down, where the mud is fine and damp, *Euplax tridentata* is dominant. Seven small uncommon species are present: *Macrophthalmus pacificus*, *M. punctulatus*, *Leipocten sordidulum*, *Cyrtograpsus* (?) *paludicola*, *Cyrtograpsus* (?) sp., *Halicarcinus australis*, and *Cleistostoma mcneilli*. Below L.W.N. the only crab is *Macrophthalmus setosus*.

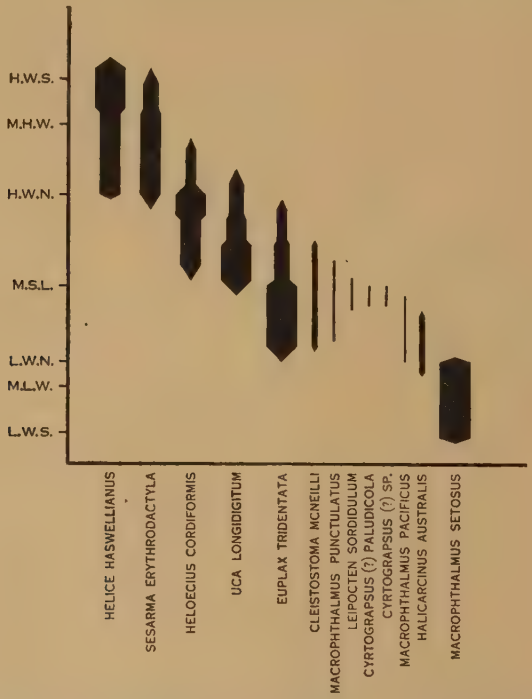

Fig. 4.—Diagrammatic representation of zonation and abundance of crabs at Bulimba. For key to densities see Figure 2.

(3) *Kangaroo Point.*—Twelve miles upstream (Fig. 5). Here *Helice haswellianus* and *Sesarma erythrodactyla* are again codominant above H.W.N. From H.W.N. to M.S.L. *Uca longidigitum* and *Heloecius cordiformis* are abundant, with *Uca* dominating in most places. From M.S.L. to L.W.N. *Cleistostoma mcneilli* is dominant. *Euplax tridentata*, which occupies this situation lower down the river, is still very common.

There are only two other species in this area, *Leipocten sordidulum* and *Halicarcinus australis*. Below L.W.N. *Macrophthalmus setosus* is the only intertidal crab.

(4) *St. Lucia.*—Eighteen miles upstream (Fig. 6 and Plate 2, Fig. 2). *Helice* does not penetrate this distance upstream, and instead the highest part of the bank is occupied by *Sesarma erythrodactyla*. From H.W.N. to M.S.L. *Uca longidigitum* and *Heloecius cordiformis* are codominants, and from M.S.L. to about L.W.S. *Cleistostoma mcneilli* is dominant. *Euplax tridentata* is reduced in number, and the only other species in this region is *Halicarcinus australis*. *Macrophthalmus setosus*, which further downstream characterizes the area below L.W.N., does not extend up the river as far as this.

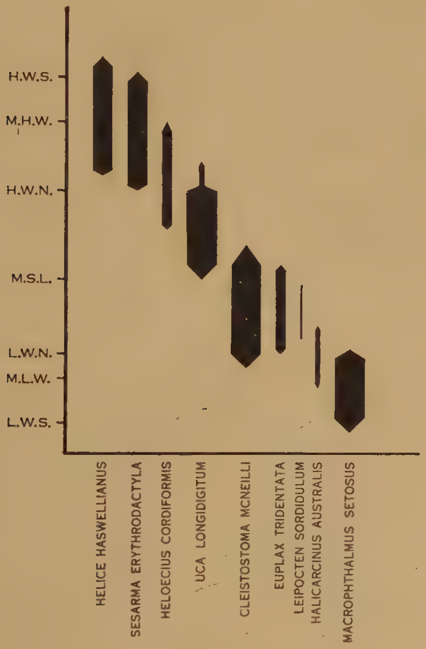

Fig. 5

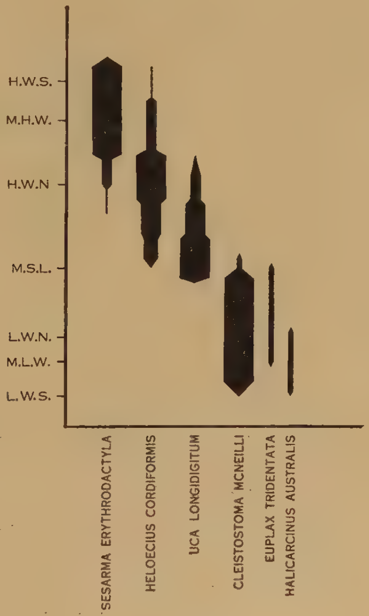

Fig. 6

Fig. 5.—Diagrammatic representation of zonation and abundance of crabs at Kangaroo Point. For key to densities see Figure 2.

Fig. 6.—Diagrammatic representation of zonation and abundance of crabs at St. Lucia. For key to densities see Figure 2.

To summarize, the general pattern of vertical distribution is:

(1) *Sesarmine Zone.*—Extending upwards from about H.W.N. The substrate is usually dry gravelly mud with loose stones. The only crabs present are *Helice haswellianus* and *Sesarma erythrodactyla*.

(2) *Ocypodine Zone* (Plate 1, Fig. 1).—From about H.W.N. to M.S.L. The crabs here are *Uca longidigitum* and *Heloecius cordiformis*. If mangroves are absent or very small and sparse, *Uca* is dominant and *Heloecius* subdominant; if mangroves are present they are codominant; if the mud is gravelly and firm *Heloecius* is dominant.

(3) *Upper Macrophthalmine Zone.*—From about M.S.L. to L.W.N., provided the usual substrate of soft fine mud is present. The dominant crab is *Euplax tridentata* in the lower reaches and *Cleistostoma mcneilli* in the higher reaches. The other species in this zone are small and not common.

(4) *Lower Macrophthalmine Zone.*—From L.W.N. to L.W.S. The mud is very soft with many shallow pools, and the only crab is *Macrophthalmus setosus*, which occurs usually in great numbers.

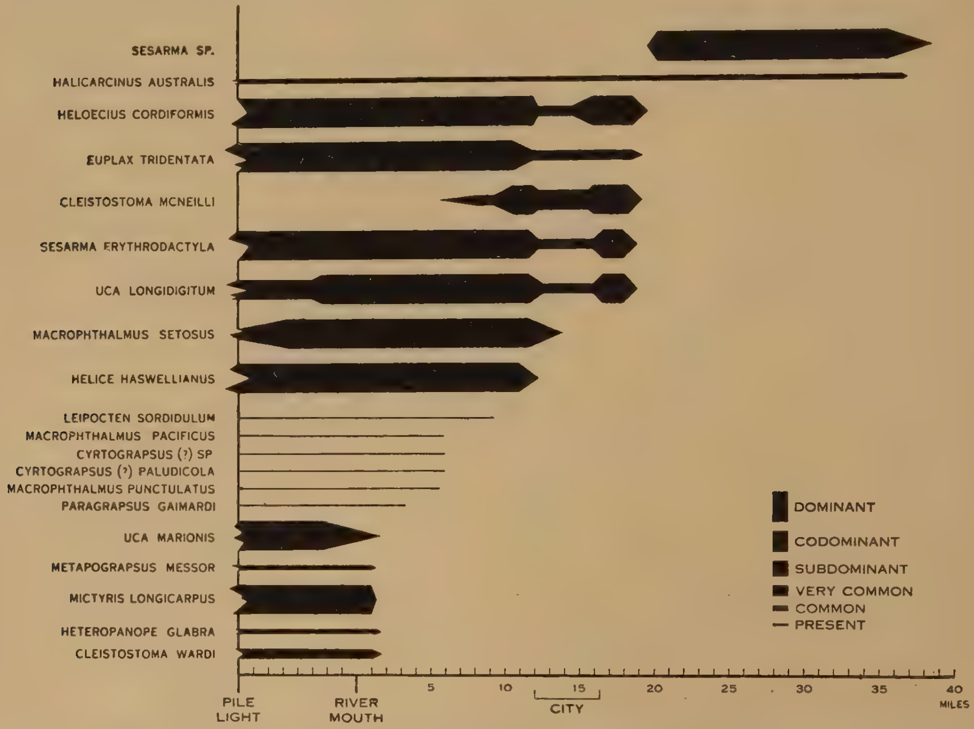

Fig. 7.—Diagrammatic representation of abundance and penetration of crabs along the Brisbane River during normal weather conditions. The number of dominants at each locality is due to the diversity of habitats.

VI. Distribution of Crabs along the Brisbane River

(*a*) *Normal Distribution*

A diagrammatic representation of the distribution during normal weather conditions is given in Figure 7.

For most of the period of investigation, i.e. from September 1956 to March 1958, no variations in distribution were observed. The number of species decreases fairly steadily as the river is ascended, excepting for the sharp drop from six species at 18 miles to two at 20 miles (Fig. 8). The last two species disappear together about 37 miles upstream, which is approximately the upper limit of mangroves (*Aegiceras corniculatum* (L.) Blanco).

It is possible that the upstream penetration of a species is limited by the availability of its preferred habitat. It is not known whether the disappearance of crabs at 37 miles is related to the disappearance of mangroves or to salinity. The absence of stones may effect the under-stone population, but since there are stones beyond the limit of all under-stone dwellers, this is not the reason for their disappearance. It must be concluded that the controlling factor is salinity. This view is strengthened by the variations caused by weather conditions.

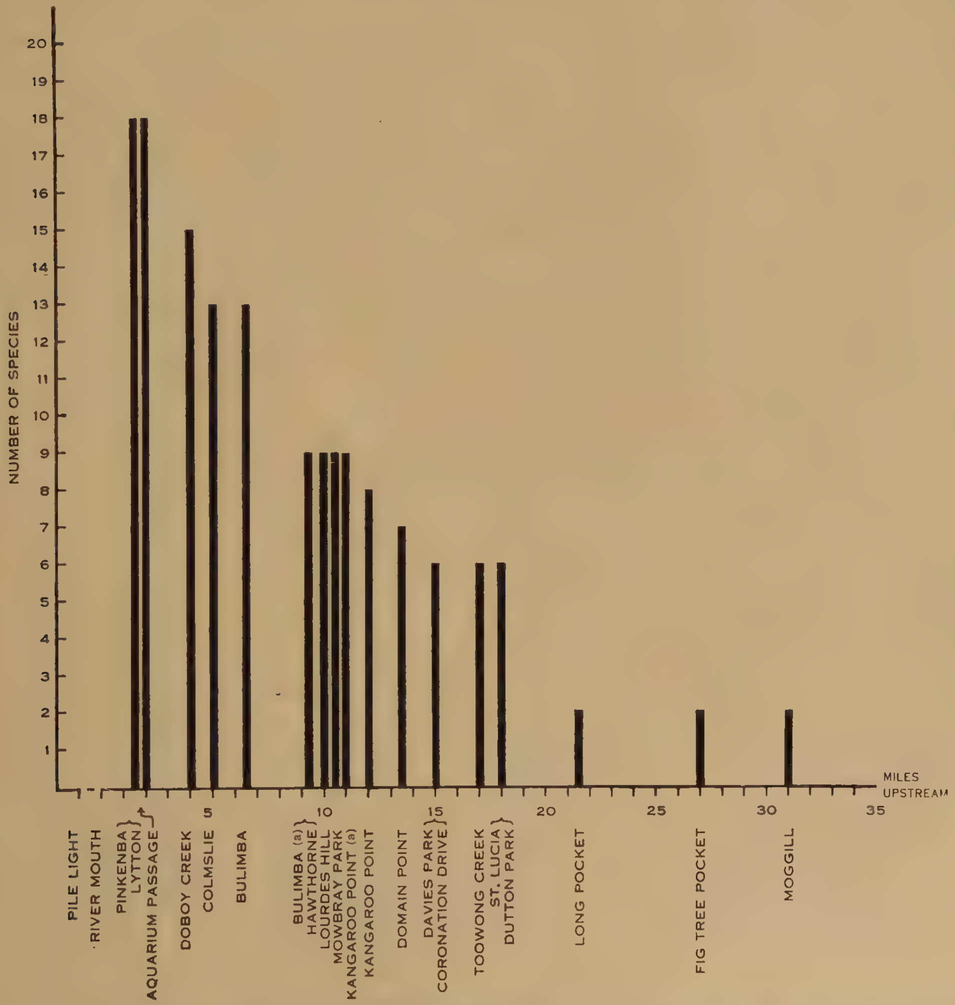

Fig. 8.—Histogram showing numbers of species of crabs at selected localities along the Brisbane River.

(*b*) *Distribution during Late Stage of Drought*

The wet season in Queensland is in summer, with the normal Brisbane rainfall for summer (January to March) *c.* 19 in. and the annual average *c.* 45 in. In 1957 and 1958 the summers were dry, with 9 and 14 in. respectively, and the total 1957 rainfall was 20½ in. This drought caused unusually high salinities in the river. Towards the end of the investigations, in May 1958, some differences in the crab distribution were noticed.

Thus at Aquarium Passage, under stones near M.S.L., several species were present that were not previously found in the river. All are inhabitants of Moreton Bay: *Thalamita crenata*, *Heteropilumnus* sp., and *Pilumnopeus serratifrons*. Besides these, anemones, ascidians, and some gastropods not usually present in the river were found. The penetration of *Cleistostoma mcneilli* also altered towards the end of the drought period. Instead of disappearing beyond 20 miles upstream its range extended as far as 29 miles.

(*c*) *Distribution after Flooding*

In June 1958, instead of the June average of 2½ in., the rainfall was 9 in., 7 in. falling in 5 days. The resulting fresh had a marked effect on the distribution as described in Section VI(*b*) above. Investigations a week after the water level had returned to normal (June 24 and 26) showed that *Cleistostoma mcneilli* extended only 20 miles upstream, i.e. exactly as before the drought. This situation was in existence when investigations ceased. Species in the lower reaches were also affected by the flood. The Bay species found at Aquarium Passage just before the rain (*Thalamita crenata*, *Pilumnopeus serratifrons*, and *Heteropilumnus* sp.) disappeared.

VII. DISCUSSION

Crabs are the dominant intertidal surface animals in the Brisbane River, and fall into well-defined zones. Whether this is so in all Australian estuaries will not be known until comparable investigations have been made elsewhere.

In Britain, a considerable amount of work has been done on estuarine ecology (Allen and Todd 1902*a*, 1902*b*; Percival 1929; Fraser 1932; Alexander, Southgate, and Bassindale 1936; Purchon 1937; Bassindale 1938, 1942; Hartley and Spooner 1938; Milne 1940; Beanland 1940; Spooner and Moore 1940; Holme 1949). This work shows that crabs are a very small part of the intertidal surface fauna in Britain, the only species found further upstream than the mouth of estuaries being *Carcinus maenas* (L.).

MacGinitie (1935) found crabs of the families Cancridae and Grapsidae in an estuary in California. Those listed are seven species of *Cancer*, *Pachygrapsus crassipes* Randall, *Hemigrapsus nudus* Dana, and *H. oregonensis* (Dana). Only one cancrid, *Cancer novae-zealandiae* has been recorded in Australia (McNeill and Ward 1930) and this is restricted to Tasmania; neither of the grapsid genera have been found. As MacGinitie did not extend his investigations beyond a few miles upstream, nor relate species to any tidal level, it is difficult to compare estuarine crabs in California with those found in the Brisbane River. However, it is clear that in California, as in Britain, crabs are a small part of the estuarine surface fauna; annelids, molluscs, and other crustaceans being relatively more numerous. This agrees with statements of Ricketts and Calvin (1948) who record mostly the same crab species throughout the Pacific coast of North America but include *Pilumnus*, *Speocarcinus*, and two species of *Uca*.

In salt flats bordering the Gulf of Mexico (Hedgpeth 1950, 1957), *Cancer* is absent and the dominant crab is *Callinectes sapidus* Rathbun. *Uca* and *Sesarma* are present in marshy or grassy borders of the ponds. This situation shows some resemblance to that of the Brisbane River.

Numerous species have been recorded from South African estuaries (Day, Millard, and Harrison 1952; Scott, Harrison, and Macnae 1952; Day, Millard, and Brockhuysen 1953; Millard and Harrison 1954; Day and Morgan 1956). Most of these occur near the mouths of estuaries and so presumably do not normally withstand great salinity variations. Only two of the intertidal species listed have been found in the Brisbane River: *Metapograpsus messor* and *Thalamita crenata*. In both cases *Scylla serrata* (Förskål) lives below tide level. The intertidal genera common to the Brisbane River and South African estuaries, but whose species are different, are *Sesarma*, *Uca*, *Cleistostoma*, and *Macrophthalmus*. Some genera common in South Africa are not found here, e.g. *Dotilla*. Day does not place the crabs in zones, but it is clear from his descriptions that in general *Sesarma* and *Cyclograpsus* (similar to *Helice*) are found furthest from low water, while further down the bank *Cleistostoma* and several species of *Macrophthalmus* are found. Most species are mentioned only in fauna lists. This distribution, then, conforms generally to that of the Brisbane River.

Verwey (1930), in Java, has worked on the fauna of mangrove areas and describes five zones, based on crustacean distribution, but which include surface and subsurface animals. Furthest from low water is the grapsid zone, then two *Uca* zones, a *Metaplax* zone, and a *Scylla* zone. The relationship of these zones to tidal level, and also to the zones described for the Brisbane River, is shown in Table 2. From this it is clear that there is a fairly close resemblance in crab distribution between Java and the Brisbane River. In both cases there are grapsids furthest from low water, then *Uca*, and then other ocypods. However, all the species, and many of the genera, are different.

The zones described above are by no means constant. The observations suggest that the main factor limiting the vertical distribution is not the period of exposure but the water content of the soil. This would account for the fact that *Euplax tridentata* is often found above H.W.S., but is restricted to situations where the mud is very wet. Similarly *Heloecius cordiformis* is only found where the mud is firm enough for its large burrows to be made. Thus the zonation pattern as outlined may become much modified.

The ocypodine zone described in Section V is not the same as the *Ocypode* zone of tropical sandy beaches described by Dahl (1953), and Stephenson, Endean, and Bennett (1958). Here the genus *Ocypode* is found in sand above H.W.S., whereas those crabs of the subfamily Ocypodinae which occur in the Brisbane River are dwellers in mud below H.W.N.

Day (1951) classifies his estuarine fauna into five groups: The freshwater component, the stenohaline marine component, the euryhaline marine component, the estuarine component, and the migratory component. He regards most of the fauna of estuaries as belonging to the euryhaline component, the stenohaline marine and estuarine forms being few, the former confined to the area near the mouth and the latter found well upstream. The freshwater and migratory components are not treated in detail by Day and have not been included in the present work. There is no truly stenohaline marine group in the Brisbane River as salinity is always variable, but the majority of the crabs apparently approximate to this category. It is difficult to apply Day's classification of the two other groups to the Brisbane River, because of the difficulty of defining the term "estuarine" (Hedgpeth 1957). The Brisbane River opens into Moreton Bay and it is difficult to mark where the estuary begins, i.e. is Moreton Bay to be considered estuarine or not? Only two of the species found in the river (*Cleistostoma mcneilli* and *Sesarma* sp.) are indisputably estuarine, as they are not present in the bay or ocean, while the others are.

TABLE 2

COMPARISON OF ZONES DESCRIBED BY VERWEY (1930) IN JAVA, AND THOSE DESCRIBED FOR THE BRISBANE RIVER

<table>
<tr><td>H.W.S. —</td><td>1
Sesarma</td><td rowspan="2">1
Sesarmine</td></tr>
<tr><td></td><td rowspan="2">2
Uca</td></tr>
<tr><td>H.W.N. —</td><td rowspan="2">2
Ocypodine</td></tr>
<tr><td></td><td>3
Uca</td></tr>
<tr><td></td><td rowspan="2">4
Metaplax</td><td>3
Upper macrophthalmine</td></tr>
<tr><td>M.S.L. —</td><td>4
Lower macrophthalmine</td></tr>
<tr><td>L.W.S. —</td><td>5
Scylla</td><td></td></tr>
</table>

The migration of an estuarine fauna either seasonally or after drought or flood, has not been investigated by most estuarine ecologists. The extension upstream of *Cleistostoma mcneilli* and the appearance in the river of bay forms during the 1957 drought, and the return to normal after the subsequent flood in June 1958, indicate that for some species at least salinity limits upstream penetration. A week after the flood, there was no change in the upstream limit of most of the crabs, which means that they can withstand a sudden drop in salinity at least for a while.

It will be noted that after two years of drought only limited upstream penetration of crabs had occurred. During this period the salinities must have been increasing, and it can be inferred that there is considerable tolerance of higher salinities, approaching oceanic levels. This is not unexpected in view of the fact that, with two exceptions, the species occur in Moreton Bay as a whole.

Fischer-Piette (1931) studied the distribution of fixed animals in French estuaries opening into the English Channel, and found considerable seasonal variation. Winter is the wet season, and during summer, when salinity is higher, the animals investigated penetrated further upstream. A very wet winter convinced him that lowered salinity is the limiting factor in estuarine distribution. He found tunicates the least resistant to variation and barnacles the most resistant.

The effect of lowered salinity on corals has been studied in Queensland. Stephenson, Endean, and Bennett (1958), reviewing literature referring to the effect of rainfall and flooding on corals at Low Isles, north Queensland, concluded that coral here is "tolerably resistant to the combined effects of freshwater and mud which accompany flooding". This seems to hold in general for coastal species (Endean, Kenny, and Stephenson 1956; Endean, Stephenson, and Kenny 1956). The exceptional flood and cyclone of 1918, however, did cause considerable damage to coral of the Great Barrier Reef (Stephenson 1956). Corals in Moreton Bay must withstand salinity variation, but the range is limited. Stephenson (1956) records that corals died in Moreton Bay after the particularly wet summer of 1955, and Slack-Smith (personal communication) has worked on this problem. Both authors believe this death to have been caused by freshwater outflow into the bay from beach drainage, creeks, and the flooded Logan River.

Teal (1958) in an investigation on *Uca* spp. found that salinity and habitat preferences are the major factors influencing their distribution.

The effects noted by all these authors, then, are similar to those found with local crabs. It is apparent in all these cases that the animals concerned are resistant to some salinity changes, but definite limits exist, particularly as regards tolerance to lowered salinities. The exact evaluation of salinity as a factor limiting animal populations requires detailed hydrological investigations which have not been carried out in Queensland.

VIII. Acknowledgments

The author is indebted to the following: Queensland Department of Harbours and Marine for salinity data; Commonwealth Meteorological Bureau for rainfall data; Dr. I. D. Hiscock for photographic assistance; and Mr. R. Kenny for advice on preparation of the figures. Especial thanks are due to Mr. F. A. McNeill of the Australian Museum and Mr. M. W. F. Tweedie of Raffles Museum for assistance in identification, and to Professor W. Stephenson who suggested the problem and offered advice and encouragement at all stages.

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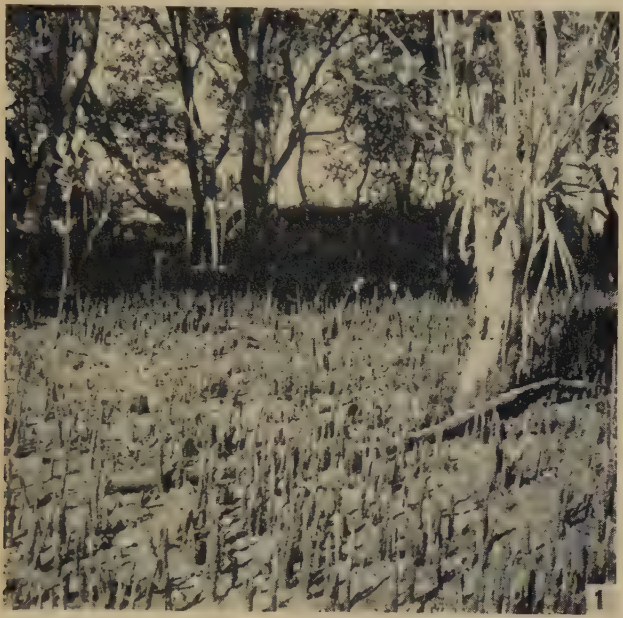
DISTRIBUTION OF INTERTIDAL CRABS IN THE BRISBANE RIVER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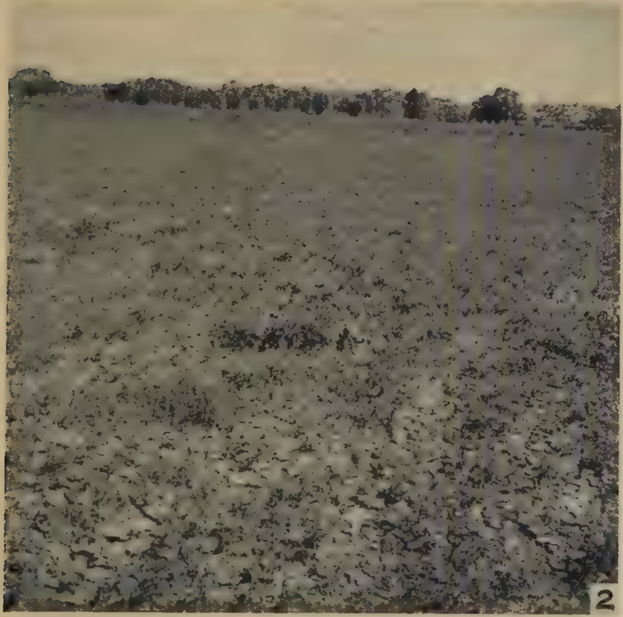
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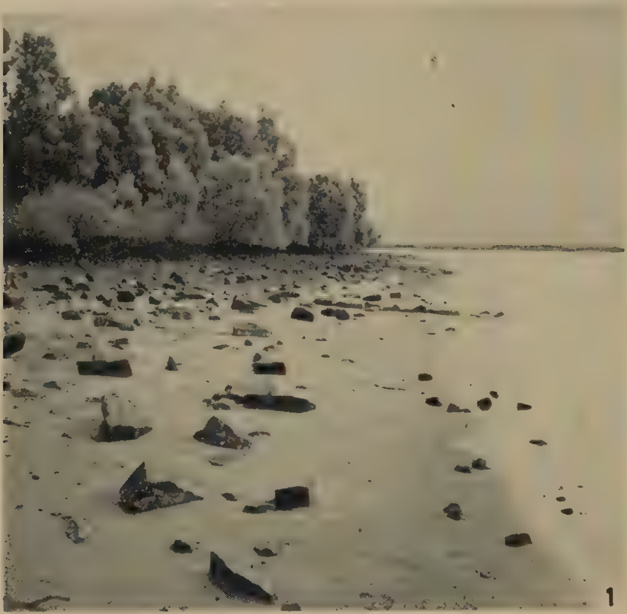
Fig. 1.—Mangrove habitat typical of lower reaches of the Brisbane River. Area shown is between M.H.W. and M.S.L., i.e. ocypodine zone.

Fig. 2.—Salt flat stretching above H.W.S. about 1½ miles from the river mouth. The river is out of sight beyond the mangroves.

DISTRIBUTION OF INTERTIDAL CRABS IN THE BRISBANE RIVER



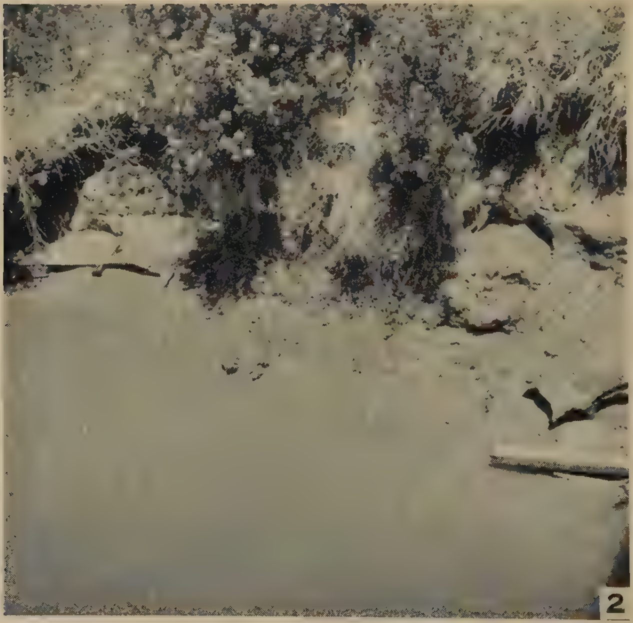
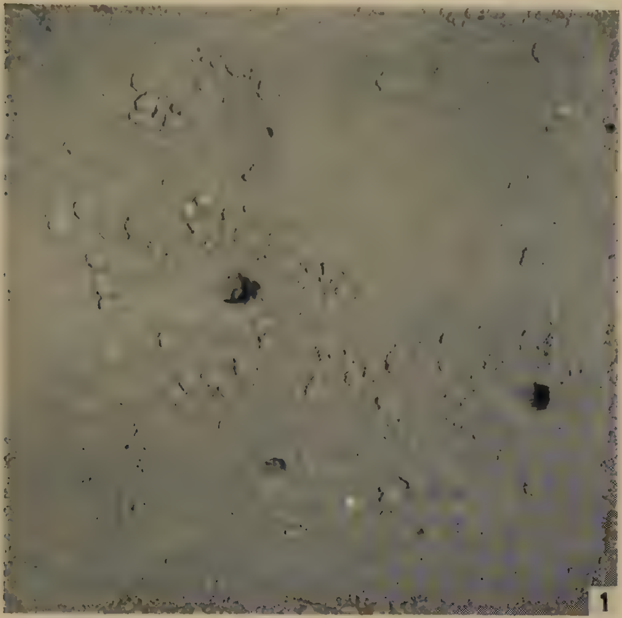


Fig. 1.—River bank at Aquarium Passage just before low tide (neap).
Fig. 2.—River bank at St. Lucia at mid tide.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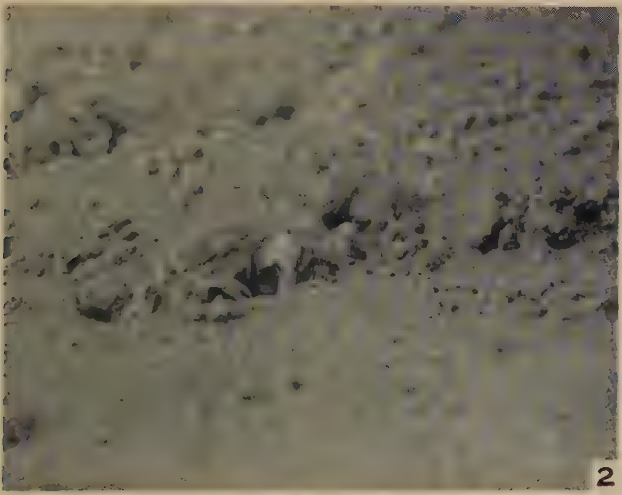
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Fig. 1.—Typical burrows of *Uca longidigitum* and *Uca marionis* at Aquarium Passage. It is very difficult to distinguish between burrows of the two species. The diameter of the largest burrow shown is about $\frac{3}{4}$ in.

Fig. 2.—Female *Uca longidigitum* emerging from its burrow.

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THE AUSTRALIAN PORTUNIDS (CRUSTACEA: PORTUNIDAE)

III. THE GENUS PORTUNUS

By W. Stephenson* and B. Campbell*

[*Manuscript received November* 13, 1958]

Summary

Thirteen species of the genus *Portunus* Weber are recorded from Australia, including one new species and five new records. These species are described and illustrated, and a key is given to known Indo-West-Pacific species. First pleopods of males are considered in detail and a key based on their features is included.

The problems of designating subgenera are discussed and the relevance of a knowledge of the structure of first male pleopods is indicated.

I. Introduction

The Indo-West-Pacific species of the genus *Portunus* Weber have not been revised since Alcock (1899), and the only comprehensive Australian treatments are Haswell's (1882*b*) outdated work, and Hale's (1927) study of the attenuated South Australian fauna.

The present paper details and discusses the Australian species, and is based upon the collections in Australian institutions up to January 1956, supplemented by recent collections made by or held at the University of Queensland. It (*a*) amends synonymies and brings them up to date (for reasons of brevity the less important older synonyms are rarely given); (*b*) includes keys to the Indo-West-Pacific species based upon general features; (*c*) includes descriptions of first male pleopods of Australian species and gives keys to the Indo-West-Pacific species based on their structure; and (*d*) revises and extends specific descriptions, including photographic illustrations of intact animals and male abdomens; and (*e*) includes a description of one new species.

Descriptions of first pleopods of the males refer to unflattened appendages as viewed from the ventral surface with abdomen uplifted. All figures are of the left pleopods, i.e. right as viewed from the under surface of the crab. It should be noted that the concave border lies to the outside of the animal and the convex towards the inside. In some cases permanent balsam mounts were made after treating with caustic potash and staining in fast green; in other cases temporary mounts were made in glycerine and alcohol. All figures of pleopods are either based upon camera lucida outlines or were drawn with the assistance of a squared micrometer eyepiece. Drawings of third maxillipeds were made similarly and again are of the left appendage, i.e. right as viewed from the under surface of the crab.

Where colour is not stated the colour of live specimens has not been recorded and that of alcohol-preserved specimens is a "washed out" shade of brown.

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II. Description of Genus and Species

Genus PORTUNUS Weber

Portunus Weber, 1795, p. 93. Fabricius, 1798, p. 325. Rathbun, 1897, p. 155. Hale, 1927, p. 149. Rathbun, 1930, p. 33 (synon.). Edmondson, 1954, p. 235. Internat. Comm. Zool. Nom., 1956, Opin. 394.

Lupa Leach, 1814, p. 390. Milne Edwards, H., 1834, p. 445. Dana, 1852*a*, p. 268. Barnard, 1950, p. 152.

Neptunus de Haan, 1833, p. 7. Milne Edwards, A., 1861, p. 314. Miers, 1876*a*, p. 23; 1886, p. 171. Alcock, 1899, p. 28 (synon.). Shen, 1937, p. 99. Sakai, 1939, p. 385.

Achelous de Haan, 1833, p. 8. Milne Edwards, A., 1861, p. 336. Barnard, 1950, p. 159.

Amphitrite de Haan, 1833, p. 8. Dana, 1852*a*, p. 277. Stimpson, 1858, p. 38 ; 1907, p. 77.

Pontus de Haan, 1833, p. 9.

Monomia Gistel, 1848, p. viii. Barnard, 1950, p. 155.

Xiphonectes Milne Edwards, A., 1873, p. 157. Doflein, 1902, p. 659.

Hellenus Milne Edwards, A., 1879, p. 221. Barnard, 1950, p. 158.

non *Portunus* Leach, 1814, p. 390.

non "*Portunus*", Palmer, 1927, p. 877. Sakai, 1939, p. 377.

The use of the name *Portunus* has been confused by its being applied to two quite different genera. This has been resolved by the International Commission on Zoological Nomenclature (1956) agreeing to suggestions from Dr. L. B. Holthuis. The genus commonly known as *Neptunus* de Haan, 1833, has thus become *Portunus* Weber, 1795. The genus commonly known as *Portunus* Fabricius, 1798, and occasionally as *Liocarcinus* Stimpson, 1870,* thus becomes *Macropipus* Prestandrea, 1833.

Further synonymy problems have arisen from the status of de Haan's genera *Achelous* and *Amphitrite*, and of A. Milne Edwards' genera *Xiphonectes* and *Hellenus*. Most recent authors relegate these to subgeneric status, with Barnard (1950) as the notable exception. Rathbun (1930) drew attention to the preoccupation of *Amphitrite*, but since then it has been used subgenerically by Shen (1937) and Sakai (1939). Here *Monomia* Gistel, 1848, should be employed.

For a fuller early synonymy at the generic level Rathbun (1930) should be consulted. The specific synonymies give the revised generic names of species previously recorded from Australia.

Generic Description (*Abbreviated*)

The nomenclature follows that of *Thalamita* cited previously (Stephenson and Hudson 1957).

Carapace.—Transverse, usually very broad, always broader than long; depressed or a little convex. Front proper relatively short ($\frac{1}{5}$–$\frac{1}{6}$ breadth of carapace excluding last anterolateral tooth). Frontal teeth usually well defined; from 3 to 6 in number, usually 4.

Anterolateral borders.—Oblique and arched, longer than posterolateral borders, typically bearing 9 regular teeth of which the last may be enlarged. (In two of the species as few as 4 teeth are present.)

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* The original paper, not consulted, is cited in Zoological Record for 1871 as "Stimpson, W., and Pourtalès, L. F. de".

Carapace surface.—Sometimes with conspicuous ridges, reminiscent of *Thalamita*, and sometimes with elevated granular areas. The terminology used in the two cases is shown in Figure 1.

Basal antennal joints.—Very short, each with its antero-external angle produced to form a lobule or spine extending into the orbit; antennal flagellum not excluded from the orbit.

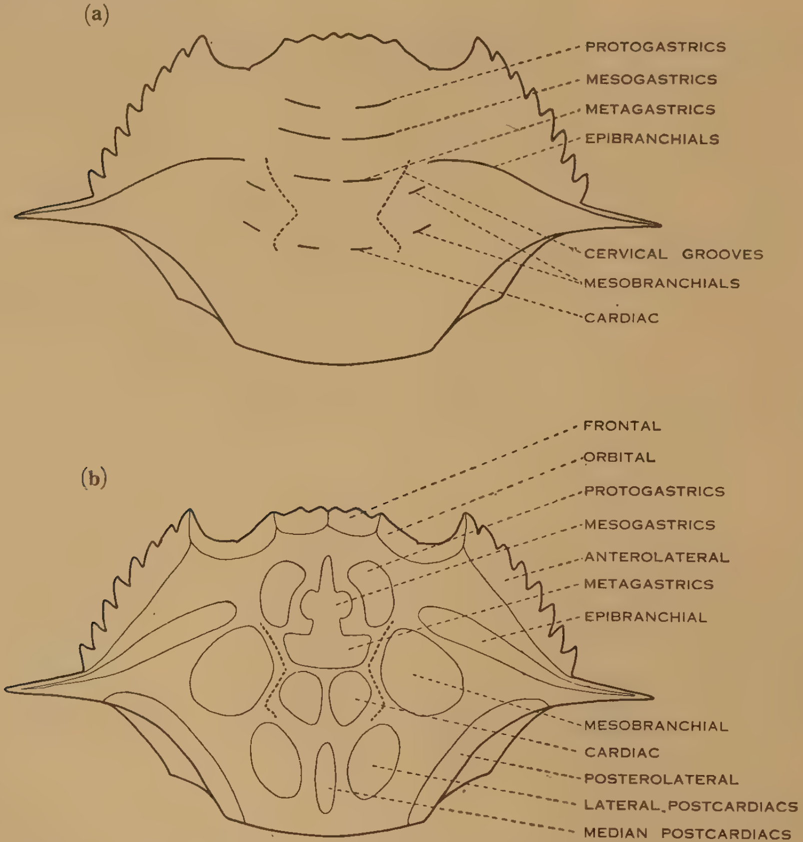
(a)
PROTOGASTRICS
MESOGASTRICS
METAGASTRICS
EPIBRANCHIALS
CERVICAL GROOVES
MESOBRANCHIALS
CARDIAC
(b)
FRONTAL
ORBITAL
PROTOGASTRICS
MESOGASTRICS
ANTEROLATERAL
METAGASTRICS
EPIBRANCHIAL
MESOBRANCHIAL
CARDIAC
POSTEROLATERAL
LATERAL POSTCARDIACS
MEDIAN POSTCARDIACS

Fig. 1.—(*a*) Designation of ridges and depressions of carapace in species of *Portunus* without elevated areas (depressions dotted).
(*b*) Designation of regions of carapace in species of *Portunus* with elevated areas (main depressions dotted).

Male abdomen and pleopods.—Third to fifth abdominal segments fused. The shapes of ultimate and penultimate segments vary and are of diagnostic value. First pair of pleopods tubular and of diagnostic value.

Chelipeds.—Equal or subequal and longer, usually much longer, than any of the legs. Anterior borders of arms spinous. Wrists with both inner and outer spines. Palms prismatic, costate, and strongly toothed.

Fifth legs.—All segments conspicuously flattened, posterior border of propodus with bristles, not spines.

Comments

Species of *Portunus* have a characteristic facies, and an "average" species can be clearly recognized to belong to the genus by virtue of: (1) broad carapace, (2) nine anterolateral teeth, and (3) costate hands. The "less average" species cause more difficulty; they comprise (i) those with relatively narrow carapace and (ii) those with less than nine anterolateral teeth.

The former (*Achelous* auct. non de Haan) are distinguishable from *Carupella* Lenz & Strunck, 1914, by having a much broader carapace and also a broader basal antennal joint. The latter are distinguishable from *Thalamita* Latreille, 1829, and all of the genus *Charybdis* de Haan, 1833,* except subgenus *Gonioneptunus* Ortmann, 1893, by the fact that the basal antennal joint does not exclude the flagellum from the orbit. *Gonioneptunus* is distinguishable from *Portunus* by the possession of six tolerably regular anterolateral teeth (as in *Charybdis* as a whole), but in morphological details and presumably in evolutionary relationships this is the group closest to *Portunus*.

Lupocyclus Adams & White, 1849, with nine anterolateral teeth, also resembles the *Lupocycloporus* group of the genus *Portunus* in having elongate chelipeds, but is distinguished from *Portunus* by having alternately long and short anterolateral teeth, and by having a very narrow basal antennal joint.

III. The Subgenera

Numerous problems arise at the subgeneric level. Commonly, and following Alcock (1899), the Indo-West-Pacific species of the genus have been divided between five subgenera, viz. *Neptunus*, *Amphitrite*, *Achelous*, *Hellenus*, and *Lupocycloporus*. Rathbun (1930) on the other hand in dealing with the American species recognized only two subgenera—*Portunus* and *Achelous*. Barnard (1950) evidently distinguished the same groups as Alcock and listed four of them in the South African fauna, but gave them generic status, viz.: *Lupa*, *Monomia*, *Hellenus*, and *Achelous*.

If one wishes to distinguish several subgenera, Alcock's names would need drastic revision as follows: for *Neptunus* de Haan, 1833, read *Portunus* Weber, 1795, the former now being invalid; for *Amphitrite* de Haan, 1833, read *Monomia* Gistel, 1848, the former being preoccupied by *Amphitrite* Mueller, 1771 (Annelida : Polychaeta); for *Achelous* Alcock, 1899, non de Haan, 1833, read *Cycloachelous* Ward, 1942 (as Rathbun (1930) has shown, the type of *Achelous* de Haan has not the lateral extension of the merus of the third maxilliped which is an important feature of Alcock's diagnosis); for *Hellenus* A. Milne Edwards, 1879, read *Xiphonectes* A. Milne Edwards, 1873; *Lupocycloporus* Alcock, 1899, stands.

Achelous de Haan is without representatives in Alcock's Indian fauna, but redefinition of subgeneric characters, following the general lines of Alcock, could lead to the establishment of a much more restricted usage than that of Rathbun (1930) with possible inclusion of one Indo-West-Pacific species.

Before a detailed nomenclatural revision is attempted, the question arises as to the real distinctness of the subgenera. A sufficient number of species exist whose characters lie across subgeneric boundaries for doubt to exist as to the utility of creating such boundaries.

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* In previous papers (Stephenson and Hudson 1957; Stephenson, Hudson, and Campbell 1957) this date was erroneously given as 1850.

The species are:

(1) *Portunus pubescens* (Dana, 1852*a*). The recent Indo-West-Pacific authors have placed this species in the subgenus *Neptunus* (e.g. Sakai 1939) or the equivalent *Portunus* (e.g. Edmondson 1954 by implication). Both Sakai and Edmondson note, however, that the carapace is not as broad as in typical members of the subgenus. A. Milne Edwards (1861, p. 342) evidently regarded the carapace as sufficiently narrow to include it in the genus *Achelous.*

(2) *Portunus oahuensis* Edmondson, 1954. This is very close to *P. vocans* (A. Milne Edwards, 1878) as described by Rathbun (1930, pp. 60–2). The latter by virtue of possessing spinous junctions of the posterior and posterolateral borders of the carapace would be referred to *Xiphonectes* = *Hellenus*. *P. oahuensis* is also very close to *Neptunus* (*Hellenus*) *nipponensis* Sakai, 1938, which again possesses spinous junctions. Edmondson's species is not described or figured as possessing the spinous junctions. Unless Edmondson's figure 20*a* is inaccurate, it can be assumed that very closely allied species would be referred to different subgenera.

(3) *Portunus tenuipes* (de Haan, 1833) has generally been referred to *Hellenus* (= *Xiphonectes*) but Sakai (1939, p. 389) justifies its transference to *Amphitrite* (= *Monomia*), following Balss (1922) on the following basis: "In general character of the carapace this species approaches the subgenus *Amphitrite* rather than *Hellenus* . . . ". In *P. tenuipes* the present authors consider the junction between the posterior and posterolateral border of the carapace to be about half-way between a rounded curve and the spinous projection typical of *Xiphonectes* = *Hellenus*.

(4) *Portunus hastatoides* Fabricius, 1798, while in other respects a typical *Xiphonectes* = *Hellenus*, has a laterally produced merus of the third maxilliped which is not characteristic of the majority.

The real difficulties which arise over the four species above suggest that it is preferable at this stage to avoid the use of subgeneric categories while dealing with the Indo-West-Pacific fauna. When the first pleopods of males are described in detail from all Indo-West-Pacific species, an independent criterion of affinities will be available, and the question could be reconsidered. Inclusion of the American fauna would be an important part of such a reconsideration because the commercially important American genus *Callinectes* Stimpson, 1860, is very close to *Xiphonectes* = *Hellenus* as regards the two major points of distinction between American species of *Portunus* and *Callinectes*, viz: ⊥-shaped male abdomen and lateral production of antero-external angle of third maxilliped (Rathbun 1930, p. 98). *Callinectes* differs from *Xiphonectes* in other important respects, but not sufficiently from the general span of the genus in the Indo-West-Pacific to have more than the status of a subgenus if such are to be recognized. The uncertain position of *Callinectes* is especially emphasized by the fact that Rathbun, the authority on the genus throughout her lifetime and one who must have been thoroughly familiar with the American forms, created one Indo-Pacific species. This species *C. alexandri* Rathbun, 1907, originally from Tahiti and Fiji, was later recorded from the Indian

Ocean (Rathbun 1911). It appears to be *Portunus pelagicus*. If the commonest and best known Indo-Pacific species of *Portunus* can be designated by an acknowledged expert as a new species of *Callinectes*, some revision of the latter is obviously desirable.

IV. Key to the Indo-West-Pacific Species Based on General Characters

Paginated references are given only for species not recorded from Australia.

1. Posterior area of carapace bearing 3 large blood-red spots, even in preserved specimens .... *P. sanguinolentus* (Herbst) (1796)
Posterior area of carapace not bearing 3 large blood-red spots 2

2(1). Hand slender, much less massive than arm 3
Hand robust, either more, or only a little less massive than arm 5

3(2). 7 spines on anterior border of arm .... *P. aburatsubo* (Balss) (1922, p. 109)
4–6 spines on anterior border of arm 4

4(3). Front with low sinuous lobes, mesogastric region with 2 granulated patches .... *P. minutus* (Shen) (1937, p. 115)
Front with 4 teeth, mesogastric region with a transverse granulated ridge .... *P. gracilimanus* (Stimpson) (1858)

5(2). Posterior–posterolateral junction of carapace either forming a right angle or a conspicuous spine 6
Posterior–posterolateral junction of carapace rounded 16

6(5). Front distinctly 4-toothed or 4-lobed 7
Front 3-toothed 14
Front either indistinctly 3-lobed ("sinuous") or flat 15

7(6). Posterior border of arm with 1 spine 8
Posterior border of arm with 2 spines 12

8(7). Stridulating apparatus on under surface of carapace parallel to and near anterolateral border .... *P. nipponensis* (Sakai) (1938, p. 301)
No stridulating apparatus present 9

9(8). Median frontal teeth nearly as large as and more prominent than laterals .... *P. tuberculosus* (A. Milne Edwards) (1861, p. 333)
Median frontal teeth very much smaller and less prominent than laterals 10

10(9). Penultimate segment of ♂ abdomen much longer than broad, with markedly concave lateral borders .... *P. macrophthalmus* Rathbun (1906, p. 871)
Penultimate segment of ♂ abdomen slightly broader than long, with markedly concave lateral borders .... *P. emarginatus*, sp. nov.
Penultimate segment of ♂ abdomen slightly longer than broad, with only very slightly concave lateral borders 11

11(10). Chelipeds very long and slender; upper surface of hand with 2 distal spines side by side .... *P. longispinosus* (Dana) (1852*a*)
Chelipeds stouter; hand with 1 distal spine .... *P. longispinosus bidens* (Laurie) (1906, p. 415)

12(7). Posterior border of merus of natatory legs serrated but without a spine .... *P. hastatoides* Fabricius (1798)
Posterior border of merus of natatory legs smooth .... *P. andersoni* (de Man) (1887*b*, p. 70)
Posterior border of merus of natatory legs bearing a spine near the distal end 13

13(12). Last anterolateral spines relatively long, so that carapace breadth (including spines) is rarely less than 2·3 times carapace length .... *P. pulchricristatus* (Gordon) (1931, p. 534)

Last anterolateral spine relatively short, so that carapace breadth (including spines) is always less than twice carapace length .... *P. spinipes* (Miers) (1886, p. 179) non Alcock (1899, p. 39)

14(6). ♂ abdomen parallel-sided for basal two-thirds .... *P. tweediei* (Shen) (1937, p. 109)

♂ abdomen with sides converging throughout its length *P. tenuipes* (de Haan) (1833, p. 39)

♂ abdomen with sides strongly concave .. *P. mariei* Guinot (1957, pp. 476–83, figs. 5–7)

♂ abdomen with sides strongly convex .... *P. alcocki* (Nobili) (1905, p. 401)

15(6). Two teeth on posterior surface of arm of cheliped .... *P. brocki* (de Man) (1887*a*)

One tooth on posterior surface of arm of cheliped .. *P. alcocki* (Nobili) (1905, p. 401)

16(5). Antero-external angle of merus of third maxillipeds not produced in a lateral direction . 17

Antero-external angle of merus of third maxillipeds strongly produced in a lateral direction 20

17(16). Carapace very broad, breadth almost twice the length 18

Carapace not very broad, breadth distinctly less than twice the length 19

18(17). Four frontal spines .... *P. pelagicus* (L.) (1766)

Two frontal spines .... *P. trituberculatus* (Miers) (1876*a*, p. 221)

19(17). Mesogastric area of carapace bearing a pair of transverse ridges; no stridulating apparatus on the under surface of the carapace .... *P. pubescens* (Dana) (1852*a*)

Mesogastric area of carapace with 4 strong tubercles; stridulating apparatus present on under surface of carapace .... *P. oahuensis* Edmondson (1954, p. 243)*

20(16). Last anterolateral spine much larger than the preceding ones; carapace moderately broad 21

Last anterolateral spine either hardly larger or even smaller than any of the others .. 25

21(20). Round, dark spot on dactyl of swimming leg .... *P. argentatus* (A. Milne Edwards) (1861, p. 332)†

No dark spot on dactyl of swimming leg 22

22(21). Arm with 1 spine on posterior border. . *P. rubromarginatus* (Lanchester) (1900, p. 746)

Arm with 2 spines on posterior border 23

23(22). Spine at inner angle of wrist enormous, two-thirds as long as palm .... *P. petreus* (Alcock) (1899, p. 37)

Spine at inner angle of wrist of normal size 24

24(25). Outer frontal teeth relatively larger; posterolateral margins of carapace relatively much shorter; penultimate segment of ♂ abdomen relatively broad .... *P. samoensis* Ward (1939, p. 4) (see footnote to *P. argentatus*)

Outer frontal teeth relatively smaller; posterolateral margins of carapace relatively much longer; penultimate segment of ♂ abdomen relatively narrow .... *P. gladiator* Fabricius (1798)

25(20). Last anterolateral spine slightly smaller than the others; carapace polished .... *P. orbicularis* (Richters) (1880, p. 153)

Last anterolateral spine slightly the largest; carapace with granular patches 26

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* This species ought to be close to *P. nipponensis* (Sakai) but does not appear to be close on those of the described features used in the present key.

† Ward (1939, p. 4) compares his *Monomia samoensis* with *N. gladiator* and the description does not mention the black spot on the dactylus which shows in his figures 5 and 6. Probably *P. samoensis* is a synonym of *P. argentatus*).

26(25). Granules on carapace in patches separated by broad smooth areas; penultimate segment of ♂ abdomen with bulging curved sides 27
Granules on carapace covering almost entire surface; penultimate segment of ♂ abdomen only slightly convex ....*P. granulatus* (H. Milne Edwards) (1834)

27(26). Eight anterolateral teeth, the third being equivalent to two normal ones; short stout ♂ pleopod ....*P. octodentata* (Gordon) (1938, p. 179)
Nine normal anterolateral teeth; ♂ pleopod relatively long and slender ....*P. orbitosinus* Rathbun (1911)

V. Key to Indo-West-Pacific Species Based on First Pleopods of the Males

The restricted nature of the key is due to the fact that the structure of the pleopods is undescribed for many species. When the pleopods are not figured in the present work a reference is given to the literature and because of uncertainties regarding these species it has been necessary to include several of them twice in the key and the final position of others may require alteration when further details are obtained. When length/breadth ratios are cited the breadth is the maximum as viewed under normal mounting and the length is as measured in a curved line from the sutures marking the origin of the distal segment.

1. Very elongate (ratio length/greatest breadth greater than 9) 2
Not very elongate 5

2(1). Smoothly, continuously, and conspicuously curved 3
Relatively straight ....*P. gladiator* (Figs. 2*J*, 3*J*)

3(2). Subterminal bristles on both sides of appendage 4
Subterminal bristles only on outside of appendage ....*P. pubescens* (Figs. 2*C*, 3*C*)

4(3). Subterminal bristles subequal ....*P. sanguinolentus* (Figs. 2*B*, 3*B*)
Subterminal bristles of two sizes, with longer and shorter ones tending to alternate in larger specimens ....*P. pelagicus* (Figs. 2*A*, 3*A*)

5(1). Very stout (ratio length/greatest breadth less than 3·5), widely flared tip, basal lobes with bipinnate hairs ....*P. granulatus* (Figs. 2*I*, 3*I*)
Either not very stout, or if so without widely flared tip or bipinnate hairs 6

6(5). Distal fourth of appendage very thin in relation to breadth (appendage relatively straight) ....*P. rubromarginatus* (Figs. 2*K*, 3*K*)
Distal fourth of appendage at most moderately thin (in most cases appendage relatively or conspicuously curved) 7

7(6). Upper surface of distal fifth of appendage bearing strong recurved spines (appendage very robust subterminally) ....*P. gracilimanus* (Figs. 2*M*, 3*M*)
Upper surface of distal fourth of appendage having (at most) spinules (appendage typically not very robust subterminally) 8

8(7). Inner surface of distal fourth of appendage bearing bristles 9
Inner surface of distal fourth of appendage bearing at most spinules 15

9(8). Right-angled bend in middle of the appendage, beyond which distal half is practically parallel-sided ....
P. argentatus (see Barnard 1950, p. 157, fig. 30*c*; Edmondson 1954, p. 238, fig. 14*c*)
If a right-angled bend in the appendage, not near the middle 10

10(9). Tip relatively blunt ....*P. nipponensis* (see Sakai 1939, p. 395, text fig. 7*c*)
Tip relatively sharp 11

11(10). Subterminal spinules on the outer side of the appendage 12
No subterminal spinules on the outer side of the appendage ....
................*P. macrophthalmus* (see Edmondson 1954, p. 241, figs. 18*e*, 18*f*)

12(11). Not more than 14 subterminal spinules on the outer side 13
Not less than 16 subterminal spinules on the outer side 14

13(12). Spinules on under surface restricted to tip .... *P. longispinosus* (Figs. 2*F*, 3*F*)
Spinules on under surface beginning approximately half-way along the appendage .... *P. emarginatus* (Figs. 2*H*, 3*H*)

14(12). Tip of appendage straight ...... *P. spinipes* (see Gordon 1931, p. 535, text fig. 10*b*)
Tip of appendage curved ("upturned") .... *P. pulchricristatus* (see Gordon 1931, p. 535, text fig. 10*a*)

15(8). Short, broad (length *c.* 3·5 times breadth), with the broadest portion about half-way up the base, sharply curving 16
Short, broad (length *c.* 3 times breadth), with the broadest portion near the base, curving 18
Relatively elongate (length *c.* 5 times breadth) with the broadest portion near the base, hardly curved .... *P. orbicularis* (see Edmondson 1954, p. 240, fig. 16*d*)
Relatively elongate (length *c.* 5–6 times breadth), with the broadest portion a little beyond the base, markedly curving 19

16(15). Subterminal spinules on the outside of the appendage 17
No subterminal spinules on the outside of the appendage .... *P. macrophthalmus* (see Edmondson 1954, p. 241, figs. 18*e*, 18*f*)

17(16). Tip of appendage straight .... *P. spinipes* (see Gordon 1931, p. 535, text fig. 10*b*)
Tip of appendage curved .... *P. pulchricristatus* (see Gordon 1931, p. 535, text fig. 10*a*)

18(15). Inner surface just beyond the basal lobes bare .... *P. octodentata* (see Gordon 1938, p. 180, figs. 4*c*, 4*c*¹)
Inner surface just beyond the basal lobes with bipinnate hairs .... *P. alcocki* (see Guinot 1957, p. 482, figs. 10*a*, 10*b*)

19(15). Subterminal spinules on both inner and outer sides of the appendage 20
Subterminal spinules or bristles only on inner side of the appendage 21
Subterminal spinules only on outer side of the appendage .... *P. tenuipes* (figs. 2*E*, 3*E*)
No subterminal spinules on either side of the appendage .. *P. orbitosinus* (figs. 2*L*, 3*L*)

20(19). Spinules on the outer side relatively dense and more numerous than on the inner side .... *P. mariei* (see Guinot 1957, p. 482, figs. 7*a*, 7*b*)
Spinules on the inner side relatively dense, more numerous than those on the outer side .... *P. brocki* (Figs. 2*G*, 3*G*)
Spinules on the inner and outer sides both relatively sparse .... *P. tweediei* (see Shen 1937, p. 112, figs. 8*c*, 8*d*)

21(19). Subterminal armature consisting of a few small spinules .. *P. hastatoides* (Figs. 2*D*, 3*D*)
Subterminal armature consisting of hairs or bristles .... *P. argentatus* (see Edmondson 1954, p. 238, figs. 14*c*, 14*d*)

VI. SPECIFIC DESCRIPTIONS

The description of the type species *Portunus pelagicus* is followed by the closely related *P. sanguinolentus* and *P. pubescens* in chronological order of description. The "*Hellenus*" group then follows in similar order, viz. *P. hastatoides*, *P. tenuipes*, *P. longispinosus*, *P. brocki*, and *P. emarginatus*. Then follows the "*Achelous*" group represented by *P. granulatus*, the "*Amphitrite*" group represented by *P. gladiator*, *P. rubromarginatus*, and *P. orbitosinus*, concluding with the "*Lupocycloporus*" group represented by *P. gracilimanus*. This allows similar species to appear adjacently.

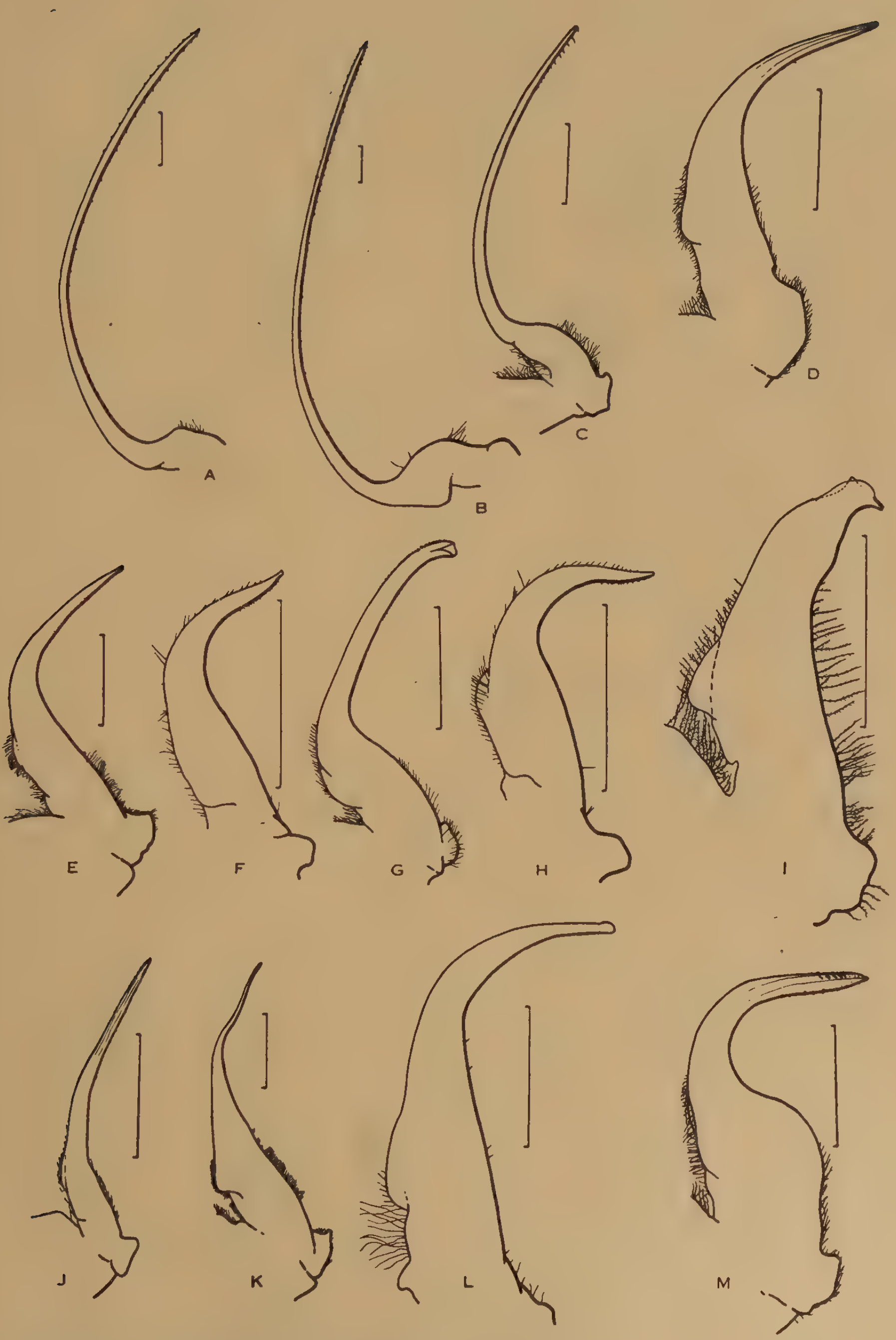

Fig. 2.—First male pleopods; outer surface on right of figure. Scale lines 2 mm. *A, P. pelagicus*; *B. P. sanguinolentus*; *C, P. pubescens*; *D, P. hastatoides*; *E, P. tenuipes*; *F, P. longispinosus*; *G, P. brocki*; *H. P. emarginatus*; *I, P. granulatus*; *J, P. gladiator*; *K, P. rubromarginatus*; *L, P. orbitosinus*; *M, P. gracilimanus.*

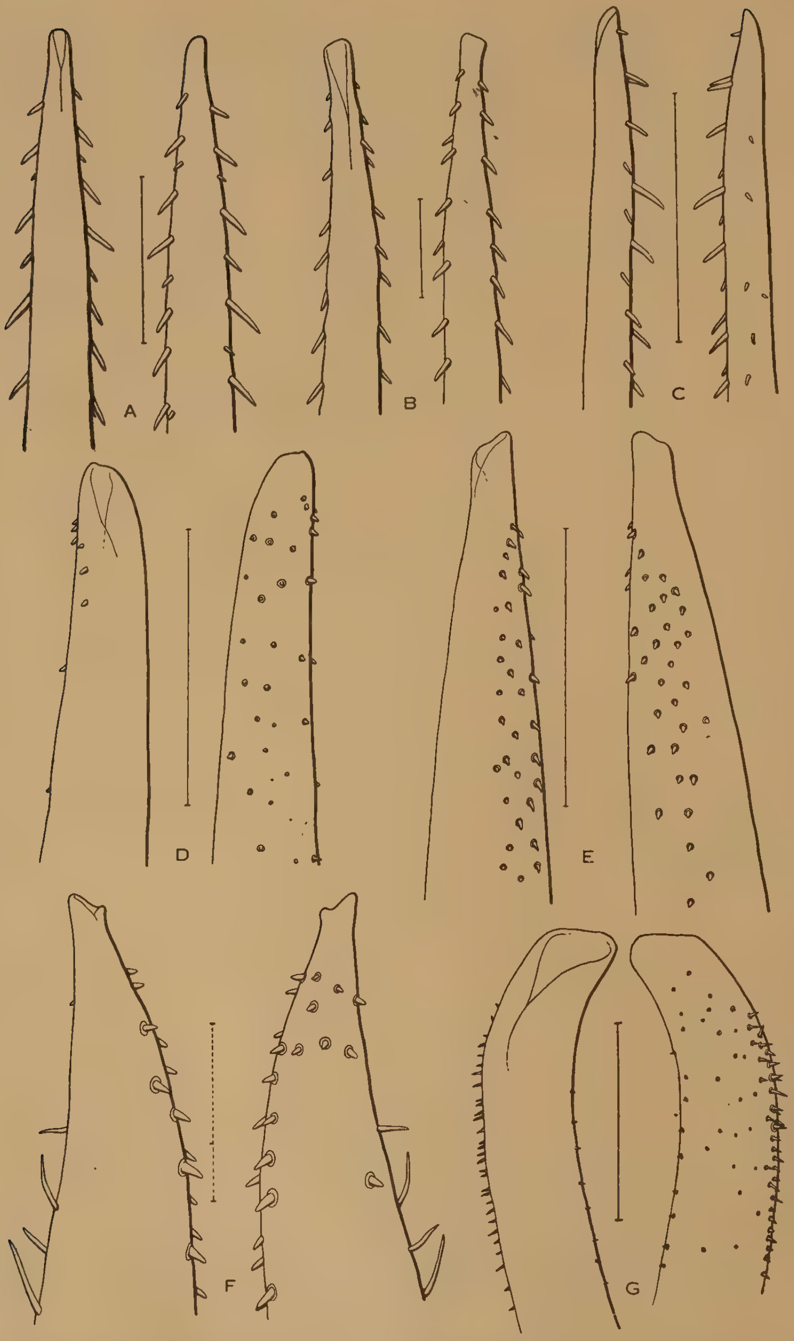

Fig. 3.—Tips of left first male pleopods. The upper surfaces are to the left of the scale lines, the lower to the right. Scale lines 0·5 mm unless otherwise stated. *A*, *P. pelagicus*; *B*, *P. sanguinolentus*; *C*, *P. pubescens*; *D*, *P. hastatoides*; *E*, *P. tenuipes* (right pleopod reversed); *F*, *P. longispinosus* (scale line 0·1 mm); *G*, *P. brocki*.

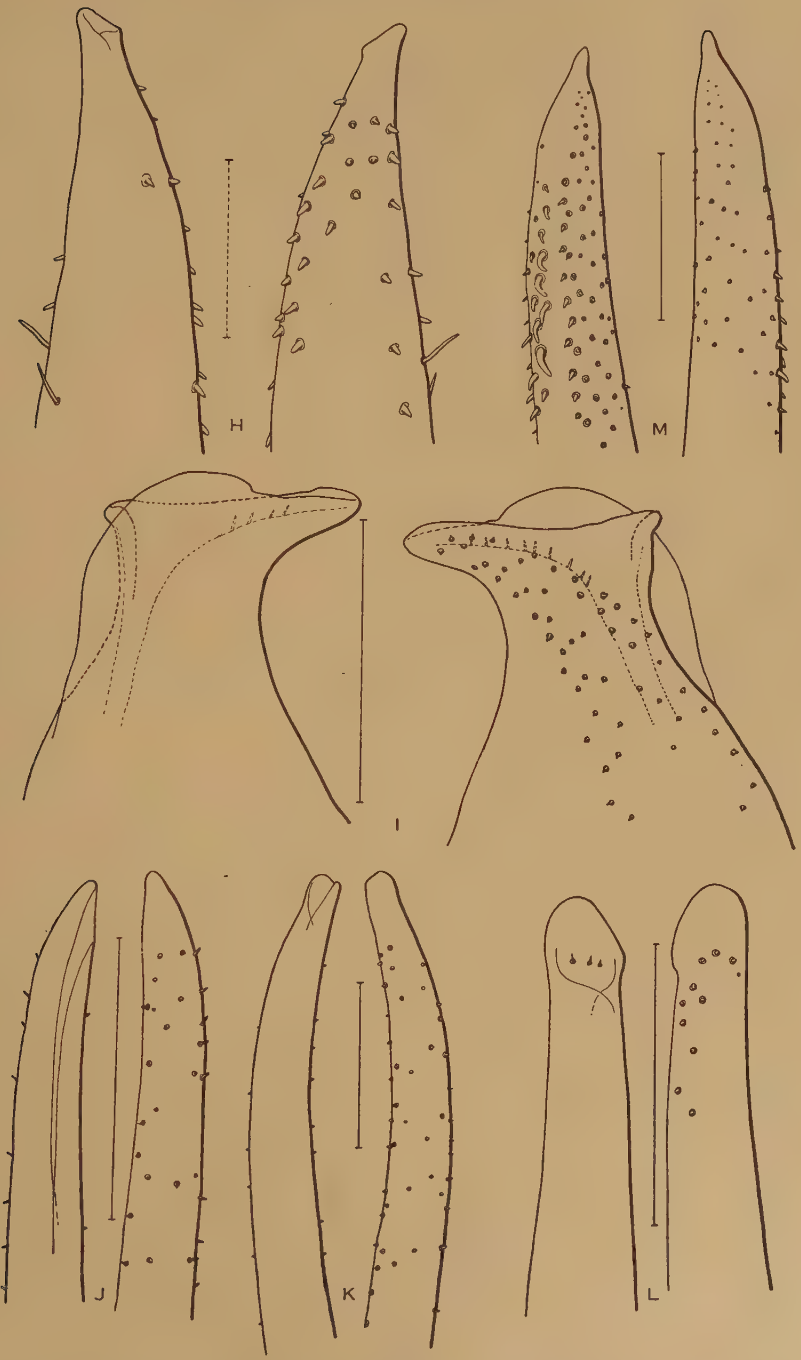

Fig. 3 (*continued*)—Tips of left first male pleopods. The upper surfaces are to the left of the scale lines, the lower to the right. Scale lines 0·5 mm unless otherwise stated. *H, P. emarginatus* (scale line 0·1 mm); *I, P. granulatus*; *J, P. gladiator*; *K, P. rubromarginatus*; *L, P. orbitosinus*; *M, P. gracilimanus*.

PORTUNUS PELAGICUS (Linnaeus)

Figs. 2*A*, 3*A*; Plate 1, Fig. 1; Plates 4*A*, 5*A*

Cancer pelagicus Linnaeus, 1766, p. 1042.

Portunus pelagicus (L.). Fabricius, 1798, p. 367. Hale, 1927, pp. 149–50, fig. 150.

Neptunus pelagicus (L.). De Haan, 1833, pp. 37–8, pls. ix, x. Milne Edwards, A., 1861, pp. 320–1. Miers, 1876*a*, pp. 25–6. Alcock, 1899, p. 34 (lit. and synon.). Calman, 1900, p. 21. Whitelegge, 1900, pp. 154–5. Boone, 1934, pp. 63–7, pls. 21–4. Sakai, 1934, p. 303. Chopra, 1935, pp. 476–7. Sakai, 1936, p. 128, pl. 38. Shen, 1937, p. 101. Sakai, 1939, pp. 387–8, pl. xlix. Chhapgar, 1957, pp. 418–9, pl. *A*, fig. 6, pl. 6, figs. *a*, *b*, *c*.

Lupa pelagica (L.). Milne Edwards, H., 1834, p. 450. Barnard, 1950, pp. 152, 153–4, fig. 27.

Portunus mauritianus Ward, 1942, p. 79, pl. 5, fig. 4.

(?) *Callinectes alexandri* Rathbun, 1907, p. 61, pl. 2, fig. 1, pl. 9, figs. 3, 3*a*, 3*b*; 1911, p. 206, pl. 17, fig. 4.

Material Examined

103 ♂♂ (9–185 mm); 54 ♀♀ (18–170 mm). Smallest ovigerous ♀ 136 mm; ovigerous ♀♀ from October; *Sacculina* infection, 1.

QUEENSLAND: 29 localities from Thursday I. to Southport. NEW SOUTH WALES: 8 localities from Coff's Harbour to Bateman's Bay. LORD HOWE I. SOUTH AUSTRALIA: Spencer Gulf. WESTERN AUSTRALIA: C. Bossut, Roebuck Bay, Exmouth Gulf, Fremantle. NORTHERN TERRITORY: Port Essington, Darwin, Groote I., Sir Edward Pellew Group.

Recorded habitats.—Intertidal, in mud and *Zostera*, shallow pools and under stones, also 3–34 fm.

Material illustrated.—♂ 70 mm, Exmouth Gulf, Dec. 1955–Feb. 1956, W. Dall and O. K. Godfrey (Zool. Dept. Univ. Qld.).

Description

Front.—Four acute tooth-like lobes of which the outer are the larger and more prominent, all lower and more rounded in juveniles.

Anterolateral teeth.—First larger than those immediately after, these becoming progressively more acute. Ninth very large and projecting straight out laterally.

Carapace.—Very broad (breadth from just over 2 to 2⅓ times length). The anterolateral borders form a broad arc whose centre lies behind the posterior border of the carapace.

Surface granulated and varying from coarse, more widely spaced granules to finer, closer ones, frequently with a short but dense pubescence between the granules. The following carapace ridges are generally recognizable: mesogastrics set at a slight angle to the antero-posterior line; epibranchials; and indistinct metagastrics. The cardiac and each of the mesobranchial areas bear a pair of low granular eminences, indistinct in the mesobranchial areas.

Chelipeds.—Elongate, massive, spinous, and ridged; under surface smooth. Posterodistal border of arm spinous, anterior border with 3 or 4, typically 4, sharp spines. Wrist with inner and outer spines. Upper surface of hand with 3 carinae, typically granular, the middle and inner ones terminating in spines, and with well-marked carinae along the middle of the inner and outer surfaces of the hand. Upper surface of movable finger typically with 3 strong carinae.

Fifth leg.—Posterior surface with fine fringing hairs, no spines or spinules.

Third maxilliped.—Antero-external angle of merus not produced laterally.

Male abdomen.—Gradually tapering, ultimate segment noticeably longer than broad.

First male pleopod.—Long, thin, curved, gradually tapering to a fine and regular tip. Beyond the basal lobes, outer surface bearing short stout spinules which are sparsest on the middle of the appendage and which continue into the terminal armature. Inner surface bare for half-way up, then showing the ends of sparsely distributed bristles which arise a little way in on the under surface. These bristles run as an irregular row to near the tip, where they fuse into the terminal armature. *Terminal bristles on both the outer and inner surfaces* are similar, being regularly arranged, stout, inclined backwards, and becoming smaller towards the tip. In larger specimens there is a roughly alternate arrangement of longer and stouter bristles.

Colour.—When alive, legs blue to lilac with white mottling, carapace purplish brown with pale mottling. After preservation in alcohol the mottling generally remains, but in various shades of brown.

Comments

There is considerable uncertainty as to the distinctness of *P. trituberculatus* (Miers 1876*b*) from the present species. Of the more recent authors Sakai (1939) kept *P. trituberculatus* separate, whereas Barnard (1950) synonymized it with the present species. To judge from Sakai's coloured plate (pl. L) the appearance in life of *P. trituberculatus* is very different from that of *P. pelagicus*, but of the diagnostic features that could be used with preserved material only the frontal teeth appear to be of much value. The other character, viz. finer granulation of the carapace, is present upon some specimens of *P. pelagicus* which have the typical colour and frontal teeth of this species.

P. pelagicus is quite the commonest of the species of this genus in shallow waters in Australia, where it forms the basis of a moderate fishery. The Queensland fishery has been commented upon by Thomson (1951) and it should be noted that the females and *Sacculina*-parasitized males are protected by law. The species is common in shallow, sandy-muddy, inshore waters, but much less common in clearer offshore waters.

According to Mr. E. M. Grant (personal communication) this species commonly rises to the surface after nightfall, swimming powerfully and purposefully, usually with the current.

Distribution

Abundantly recorded in published and present records from within Australia (Haswell 1882*b*; Ortmann 1894; Stead 1898; Calman 1900; Whitelegge 1900; Etheridge and McCulloch 1916; Rathbun 1923, 1924; Hale 1927; Yonge 1930;

Boone 1934; Chopra 1935; Ward 1937; Thomson 1951; Dakin, Bennett, and Pope 1952). The only published record located from Victoria is Ward's (1929, p. 79) statement: "The edible blue crab is recorded from the Bay" (Port Phillip). It is apparently common in Victoria (Miss J. Hope Macpherson, personal communication).

From East Africa (Barnard 1950) to Tahiti and Japan (Sakai 1939) and the Philippines (Miers 1876*a*). At the fringe of the West Pacific area at Hawaii the species seems to be absent (Edmondson 1954). It has migrated through the Suez Canal to the Mediterranean (Holthuis 1956).

PORTUNUS SANGUINOLENTUS (Herbst)

Figs. 2*B*, 3*B*; Plate 1, Fig. 2; Plates 4*B*, 5*B*

Cancer sanguinolentus Herbst, 1796, p. 161, pl. viii, figs. 56, 57.

Portunus sanguinolentus (Herbst). Fabricius, 1798, p. 367. Rathbun, 1906, p. 870. Hale, 1927, p. 150, fig. 151. Shen, 1932, pp. 34–6, figs. 2, 3, pl. 7, fig. *a*. Edmondson, 1954, pp. 236–7, figs. 12, 13.

Neptunus sanguinolentus (Herbst). De Haan, 1833, p. 38. Milne Edwards, A., 1861, pp. 319–20. Miers, 1876*a*, p. 26. Alcock, 1899, pp. 32–3 (synon.). Calman, 1900, p. 21. Chopra, 1935, p. 475. Boone, 1938, pp. 223–5, pls. 81–3. Sakai, 1939, p. 387, pl. xlviii, fig. 1. Chhapgar, 1957, pp. 417–8, pl. *A*, fig. 3, pl. 4, figs. *m–o*.

Lupa sanguinolenta (Herbst). Milne Edwards, H., 1834, p. 451. Dana 1852*a*, pp. 271–2. Barnard, 1950, pp. 152, 154–5.

Material Examined

20 ♂♂ (15–145 mm); 16 ♀♀ (24–134 mm). Ovigerous female 122 mm.

QUEENSLAND: Kennedy Sd., Darnley I., Endeavour R., Port Curtis, Double I. Pt., Moreton Bay (Deception Bay, Sandgate). NEW SOUTH WALES: Port Jackson, Broken Bay, Parramatta R. WEST AUSTRALIA: Exmouth Gulf, Geraldton.

Recorded habitats.—None recorded with specimens.

Material illustrated.—Carapace, male abdomen, third maxilliped: ♂ 117 mm, Deception Bay, 24.iii.1951, Patricia Roberts (Zool. Dept. Univ. Qld.). Male pleopod: ♂, 115 mm, Woody Pt., 18.ix.1954, E.M.G. (Zool. Dept. Univ. Qld.).

Description

Front.—Four lobes just less than right angles in small specimens and more acute in larger specimens. Outer lobes broader but barely more projecting than the inner ones.

Anterolateral teeth.—First longer and much more pointed than those immediately after (at least in unworn specimens). Next 7 more or less the same size and shape, while the last is very large and projects straight out laterally.

Carapace.—Very broad, in females breadth about $2\frac{1}{4}$ times and in males $2\frac{1}{4}$–$2\frac{1}{2}$ times length. The anterolateral borders form a broad arc whose centre lies well behind the posterior border of the carapace. Surface finely granular anteriorly, becoming smooth posteriorly. The following carapace ridges are present: mesogastrics, almost joined, forming an arc concave anteriorly; epibranchials; and metagastrics.

Chelipeds.—Elongate, spiny, and ridged; under surface smooth. Posterodistal border of arm smooth, anterior border with 3 or 4 sharp spines. Wrist with inner and outer spines. Upper surface of hand with 3 smooth carinae, the inner ones terminating in spines, and with well-marked carinae along the middle of the inner and outer surfaces of the hand. Fingers very long.

Fifth leg.—Posterior surface with fine fringing hairs, no spines or spinules.

Third maxilliped.—Antero-external angle of merus not produced laterally.

Male abdomen.—Gradually tapering, ultimate segment rounded, as broad as long.

First male pleopod.—Long, thin, curved, gradually tapering to a fine and regular tip. Outer surface bare for the proximal half, then with backwardly directed spines sparsely arranged, which gradually become larger and merge with the terminal armature. Inner surface bare for the proximal three-quarters, then a row of backwardly directed spines which merge with the terminal armature. *Terminal bristles on outer side* stout, regularly arranged, backwardly directed, and of reasonably uniform size. *Terminal bristles on inner side* stout backwardly directed bristles in 2 rows. The row on the extreme lateral surface consists of only some 5 or 6 bristles, but a more abundant row coming from the under surface projects laterally. Both rows appear lateral in a flattened mount.

Colour.—After prolonged preservation in alcohol, brown with three dark blood-red spots on the hinder end of the carapace. There are similar markings on certain of the cheliped joints, as shown in Plate 1, Figure 2. Variable amounts of red are present on the fingers.

Comments

After *P. pelagicus* this is the commonest conspicuous member of the genus in Australia. Typically it occurs in deeper water and cleaner habitats, from which it is brought to surface on rod and line.

According to Mr. E. M. Grant (personal communication) it ascends to the surface at night and swims as does *P. pelagicus*. It is highly prized as food.

Distribution

Published and present records within Australia are from Queensland (Haswell 1882*b*; Calman 1900; Grant and McCulloch 1907; Rathbun 1923), New South Wales (Haswell 1882*a*, 1882*b*), South Australia (Hale 1927), and West Australia (Rathbun 1924).

From East Africa (Barnard 1950) through the Indo-Pacific to Hawaii (Edmondson 1954). Babić (1911) records this species from the Adriatic, where presumably it had been accidentally introduced.

PORTUNUS PUBESCENS (Dana)

Figs. 2*C*, 3*C*, Plate 1, Fig. 3; Plates 4*C*, 5*C*

Lupa pubescens Dana, 1852*a*, pp. 274–5, pl. 16, fig. 9; 1852*b*, p. 84.

Achelous pubescens (Dana). Milne Edwards, A., 1861, p. 342.

Neptunus tomentosus Haswell, 1882*a*, p. 547; 1882*b*, p. 78.

Portunus pubescens (Danà). Rathbun, 1906, p. 870, pl. 14, fig. 1. Edmondson, 1954, pp. 237–8, figs. 12, 13.

Neptunus pubescens (Dana). Sakai, 1934, p. 303; 1939, pp. 388–9, pl. lxxx, fig. 1.

Material Examined

QUEENSLAND: ♂ 33 mm Murray I., Aug.–Oct. 1907, C. Hedley and A. R. McCulloch (Aust. Mus. Reg. No. P2830). NEW SOUTH WALES: ♂ 31 mm, Port Jackson, old coll. (Aust. Mus. cabinet G, drawer 14).

Material illustrated.—Murray I. specimen mentioned above.

Description

Front.—Four bluntly rounded lobes of which the outer are slightly the larger; all protruding well forward of the rounded inner orbital lobes.

Anterolateral teeth.—First broad and large, next 7 equal and sharp, the last distinctly the longest and stoutest, and projecting slightly forward.

Carapace.—Moderately broad (breadth *c.* 1·63 times length). The anterolateral borders form an arc whose centre lies approximately on the posterior border of the carapace. Carapace covered by a short dense pubescence which on removal reveals microscopic granulation and the following ridges: continuous bow-shaped mesogastric, epibranchials, and metagastrics.

Chelipeds.—Pubescent, reasonably short and stout, very spiny, under surface microscopically granulated. Posterodistal border of arm smooth, anterior border with 3 spines. Wrist with 2 spines on the outer side, a carina on the upper surface terminating in a spiniform process, and the 2 usual spines at the hand articulation, the inner of these 2 being very long. Upper surface of hand with 3 carinae, of which the middle and inner are very conspicuous and end in long spines. Well-marked carinae on inner and outer surfaces of hand.

Fifth leg.—Posterior surface with fine fringing hairs, no spines or spinules.

Third maxilliped.—Antero-external angle of merus not produced laterally.

Male abdomen.—Gradually tapering, ultimate segment 1½ times as long as broad.

First male pleopod (based on a single specimen).—Long, thin, curved, gradually tapering to an obliquely ending tip. Beyond the basal lobes the outer surface is bare for the proximal fourth, then bears a row of backwardly directed spines which increase regularly in size. Behind the tip this row passes to the under surface. Inner surface bare for proximal two-thirds, then begins a row of spinules which increase to short outwardly directed spines, these terminating well back from the tip. *Terminal bristles on the outer surface* stout, backwardly directed, and in general becoming larger and more widely spaced towards the tip. *Terminal bristles on the inner surface*: none present, and no signs of accidental loss.

Comments

Haswell's (1882*a*) separation of *Neptunus tomentosus* from *P. pubescens* is based upon the former having more rounded frontal teeth and shorter anterolateral teeth.

In Sakai's (1934) figured specimen and in the present specimens the frontal teeth are reasonably rounded. This and the slightly shorter anterolateral teeth are well within the range of variation to be expected within a single species. The dried specimen in the older collections of the Australian Museum labelled "*Neptunus tomentosus*" is most probably Haswell's type, and can be referred to *P. pubescens* without hesitation.

Haswell's specific description gives eight instead of the usual nine anterolateral teeth; nine are present in the above specimen. As Gordon (1938) has pointed out, Haswell probably excluded the outer orbital lobes in his count. If so, this would be an error of haste or oversight, because Haswell (1882*b*, p. 76) lists as a feature of *Neptunus* "latero-anterior margins with nine or more teeth (including the external orbital angle) . . . "

Distribution

Previously recorded in Australia from Port Jackson (Haswell 1882*a*, 1882*b*). Hawaii; "not uncommon on the reef . . . where it conceals itself in the sand" (Edmondson 1954). The Sandwich Is., Japan; "mud or sandy mud, 20 to 30 metres deep" (Sakai 1939).

PORTUNUS HASTATOIDES Fabricius

Figs. 2*D*, 3*D*; Plate 1, Fig. 4; Plates 4*D*, 5*D*

Portunus hastatoides Fabricius, 1798, p. 368.

Neptunus (*Amphitrite*) *hastatoides* (Fabricius). De Haan, 1833, pp. 39–40, pl. 1, fig. 3. De Man, 1895, pp. 557–8.

Neptunus (*Hellenus*) *hastatoides* (Fabricius). Alcock, 1899, pp. 38–9 (synon.). Laurie, 1906, pp. 414, fig. 8. Sakai, 1934, p. 303. Chopra, 1935, pp. 477–8. Sakai, 1936, p. 130. Shen, 1937, pp. 106–7. Sakai, 1939, pp. 391–2, pl. xlvii, fig. 1.

Neptunus (*Hellenus*) *hastatoides* var. *unidens* Laurie, 1906, pp. 414–5.

Hellenus hastatoides (Fabricius). Barnard, 1950, pp. 158–9.

Material Examined

16 ♂♂ (17–47 mm); 5 ♀♀ (21–39 mm). Ovigerous ♀ 30 mm Dec.-Feb.

QUEENSLAND: Magnetic I., near Townsville, Moreton Bay (Woody Pt., Pearl Banks). WEST AUSTRALIA: Roebuck Bay, Ninety-Mile Beach between Cape Jaubert and Wallal, Exmouth Gulf. NORTHERN TERRITORY: Darwin.

Recorded habitats.—Trawled and dredged in soft mud, sandy mud, and shelly mud, 3–9 fm.

Material illustrated.—♂ 43 mm, 3½ miles S. Woody Pt. pier, 2.xi.1952, E.M.G. (Zool. Dept. Univ. Qld.).

Description

Front.—Four acute but somewhat rounded lobes, of which the outer are very much larger than the inner.

Anterolateral teeth.—Increasing in acuteness from front to rear, with the last a very long sharp spine directed straight outwards.

Carapace.—Very broad (breadth from 2 to 2·4 times length). The anterolateral borders merge into the ninth anterolateral tooth to form a *concave* arc. Posterior–posterolateral junction an acute spine. Surface with conspicuous elevated granular areas, almost hidden by a dense pubescence in some specimens. Granules on elevated areas smooth, rounded and regular. All the areas indicated in Figure 1*B* are recognizable, with the protogastrics and mesogastrics practically confluent. Mesobranchials resolvable into 3 areas. Posterolaterals confluent with epibranchials.

Chelipeds.—Elongate, slender, with rounded granules sometimes obscured by a dense felting, but always visible on the under surface. Posterodistal end of arm with 2 long sharp spines, anterior border with 4 spines. Upper surface of wrist with granulated carinae, 2 usual spines present. Hand long and slender, upper surface with 3 low granulated carinae, of which only the inner terminates in a spine. Carina on outer surface of hand well developed, but that on inner surface relatively ill developed. Fingers very long and slender.

Fifth leg.—Posterodistal border of merus serrated. Remaining segments bearing only hairs.

Third maxilliped.—Antero-external angle of merus strongly produced in a lateral direction.

Male abdomen.—⊥-shaped, penultimate segment twice as long as broad.

First male pleopod.—Short, stout, strongly curved. Beyond the basal lobes apparently bare on both sides up to the terminal armature. Inner surface actually bears minute, almost invisible, sparsely distributed, short fine hairs. On the under surface spinules begin as a single row about half-way up the appendage, this widening into a scattered field covering the entire under surface and merging with the terminal armature. *Terminal bristles* short, stout spinules directed slightly backwards. These are sparsely and irregularly distributed on the under surface and come to the lateral surfaces near the tip, where approximately 2 are visible on the inner surface and one on the outer.

Comments

In spite of the paucity of previous Australian records, this species has appeared fairly commonly in recent collections from the warmer inshore waters around the continent. Sakai gives its habitat as " . . . muddy bottoms 30 to 100 metres deep".

The ornamentation of the posterodistal border of the merus of the fifth leg is diagnostic.

Distribution

Previous Australian records are: Friday I., Torres Strait, Arafura Sea (Miers 1884); North Australia (Henderson 1893).

From the coast of Zululand (Barnard 1950) to Japan (Sakai 1939) and the Philippines (Balss 1922), but not from the Red Sea (Stephensen 1945) nor Hawaii (Edmondson 1954).

PORTUNUS TENUIPES (de Haan)

Figs. 2*E*, 3*E*; Plate 2, Fig. 1; Plates 4*E*, 5*E*

Amphitrite tenuipes de Haan, 1833, p. 39, pl. 1, fig. 4. Haswell, 1882*b*, p. 83.

Neptunus tenuipes (de Haan). Milne Edwards, A., 1861, pp. 335, 339. Ortmann, 1893, p. 74.

Neptunus (*Amphitrite*) *tenuipes* (de Haan). Thallwitz, 1891, p. 48. Sakai, 1939, pp. 389–90, pl. lxxx, fig. 2.

Neptunus (*Hellenus*) *tenuipes* (de Haan). Alcock, 1899, p. 42. Shen, 1937, p. 104, figs. 4, 8.

Material Examined

QUEENSLAND: ♀ 16 mm, Albany Passage, Cape York, Aug.–Oct. 1907, C. Hedley and A. R. McCulloch (Aust. Mus. Reg. No. P3118); ♀ 13 mm, fragmented, near Booby I., dip net and submarine light on surface, "Stanley" trawler, 21.x.1949, collection G. P. Whitley (Aust. Mus.); ♂ 40, ♂ 42 mm near Batt Reef, 1.iv.1958, otter trawl in 20 fm on coral sand bottom, collection N. Haysom, *Challenge* survey (Zool. Dept. Univ. Qld.). WEST AUSTRALIA: ♂ 42 mm, Exmouth Gulf, June–Sept. 1954, per Fisheries Division, C.S.I.R.O., otter trawl, 5–10 fm (Zool. Dept. Univ. Qld.); ♂ incomplete, Lugger Cove, Cygnet Bay, NW. Australia, surface dip net and lamp, 15.x.1949, pres. C.S.I.R.O. Fisheries Division (Aust. Mus. Reg. No. P12499).

Material illustrated.—Exmouth Gulf specimen, see above.

Description

Front.—Three-toothed, with all teeth somewhat projecting, the laterals much broader than the median.

Anterolateral teeth.—First broad and blunt, the next 7 increasing in sharpness, the last much the longest and directed slightly backwards.

Carapace.—Moderately broad (breadth twice or just less than twice length) with very large orbits. Anterolateral borders form a curve whose centre lies just behind the cardiac region. Posterior–posterolateral junction elevated to form a short ridge bearing an almost right-angled border. Surface with well-defined granular elevations, between which is a fine pile of hairs. All the areas shown in Figure 1*B* are present and in addition a pair of postfrontals. The protogastric is almost split into 2 areas, the mesogastric is split into 3, the metagastric into 2, and the mesobranchial into 3 or 4. There are 2 distinct anterolateral clumps and a small posterolateral. The posterior border of the carapace is beaded.

Chelipeds.—Elongate, with granules showing through a tomentum on the upper surface and with granules or squamiform markings on the under surface. Posterodistal border of the arm bearing 1 spine, sometimes almost obsolescent, anterior border bearing 3 or 4 spines. Wrist with the 2 usual spines and granular carinae. Upper surface of hand bearing 3 granular carinae, of which only the innermost ends in a spine. Dactyl with granular carinae on upper surface.

Fifth leg.—Posterodistal border of merus finely serrated.

Third maxilliped.—Antero-external angle of merus with a flattened expansion directed more forwards than laterally.

Male abdomen.—Penultimate segment tapering abruptly and with slightly concave borders in distal third. Ultimate segment much longer than broad, and broadly rounded. (In Shen's (1937) figure 4*b* the ultimate segment is only slightly longer than broad, and much shorter than in the present specimens.)

First male pleopod.—Short, stout, moderately strongly curved, with a slightly transverse tip. Beyond the basal lobes short, stout, backwardly directed spinules begin as a single row on the under surface of the appendage, about one-third of the way up from the base, and spread to form a wide band covering the under surface almost to the tip and spreading to give the terminal armature. *Terminal bristles on the outer side:* in one specimen, evidently relatively undamaged, the short backwardly directed spinules of the under surface appear in lateral view about two-thirds of the way up, a total of *c.* 27 being visible. In another specimen (the largest) only *c.* 6 are visible. Shen (1937, fig. 8*a*) shows 13 such bristles. *Terminal bristles on the inner side:* in both specimens 4–5 spines from the under surface are visible in lateral view behind the tip. Shen (1937, fig. 8*b*) shows 2 such bristles.

Comments

This species is particularly difficult to fit into any of the accepted subgenera, in that the antero-external angle of the third maxillipeds is not produced laterally to anything like the extent of either *Monomia* = *Amphitrite* or *Xiphonectes* = *Hellenus*. It is probably closer to *Xiphonectes*, but is atypical in a second important character, viz. the junction between posterior and posterolateral borders of the carapace is not an acute spine but much closer to a right-angled or even slightly obtuse-angled ledge.

Distribution

The only previous Australian records are from Bowen and Darnley I. (Haswell 1882*b*). From the central part of the Indo-West-Pacific area ranging from the Andamans (Alcock 1899) to Japan and the Philippines (Sakai 1939).

PORTUNUS LONGISPINOSUS (Dana)

Figs. 2*F*, 3*F*; Plate 2, Fig. 2; Plates 4*F*, 5*F*

Amphitrite longispinosa Dana, 1852*a*, pp. 277–8, pl. 17, fig. 2; 1852*b*, p. 84.

Amphitrite vigilans Dana, 1852*a*, p. 278; 1852*b*, p. 84.

Neptunus longispinosus (Dana). Milne Edwards, A., 1861, pp. 337, 339.

Xiphonectes leptocheles Milne Edwards, A., 1873, p. 159, pl. iv, fig. 1.

Neptunus (*Hellenus*) *longispinosus* (Dana). Alcock, 1899, pp. 40–2 (lit.; synon. doubtful). Sakai 1939, pp. 392–3, pl. lxxxi, fig. 4.

Portunus (*Xiphonectes*) *longispinosus* (Dana). Rathbun, 1906, p. 871, pl. xii, fig. 6. Edmondson, 1954, pp. 241–2, figs. 18, 19.

Material Examined and Illustrated

LORD HOWE I.: ♂ 14 mm, ♀ *c.* 17 mm (fragmented), 4 fm, coll. A. A. Livingstone, April 1933 (Aust. Mus. Reg. No. P10335).

Description

The description is a composite one taken from the two specimens, both of which are incomplete.

Front.—Four-lobed, all lobes low-set and rounded, the laterals very much broader than the medians.

Anterolateral teeth.—In both specimens 8 on the right, the fourth of those normally present being missing; 9 on the left, of which the fourth is very small and the sixth also small. The first tooth is blunt, the last is very elongate, and the remainder vary in length and sharpness.

Carapace.—Very broad (breadth *c.* 2½ times length). The anterolateral borders (excluding the ninth tooth) form a fairly narrow arc whose centre lies just behind the cardiac region. Posterior–posterolateral junction an elevated region with an angle of approximately 90°. Carapace with elevated granular areas, the main ones being: gastric, 2 epibranchials, cardiac, 3 postcardiacs, and 2 posterolaterals. Within these the protogastrics are each 2 ill-defined areas, the lateral portions of the mesogastrics are distinctly separated from the central portion, the metagastrics are a pair of granular crests, and the cardiacs are conspicuously elevated and separated in the mid line. The anterolaterals are diffuse, the epibranchials a granulated crest, the mesobranchials each have 2 ill-defined granular areas, while the posterolaterals are larger and more conspicuously elevated than usual.

Chelipeds.—Elongate and slender. Posterodistal border of arm with a single spine, anterior border with 4 spines. Wrist with 2 usual spines, of which the inner is much the larger. Upper surface of hand with 3 carinae, of which the 2 inner ones end in spines.

Fifth leg.—Posterodistal border of merus very finely serrated.

Third maxilliped.—Antero-external angle of merus produced forwards.

Male abdomen.—Penultimate segment tapering gently, with slightly concave borders and slightly longer than broad. Ultimate segment rounded and slightly longer than broad. (There are minor differences between the shape of the male abdomen of the present specimens and Rathbun's (1906, fig. 30), e.g. curvature of boundary between ultimate and penultimate segments.)

First male pleopod.—Short and robust, curving smoothly but sharply to an oblique and slightly flared tip. Beyond the basal lobes on the outer surface bare to just behind the tip. Inner surface bare for the first third, from there to the end there is a regular series of 13 hairs of which the first 2 point outwards and the remainder towards the tip. *Terminal bristles on the outer side:* 14 spinules in 2 rows extending almost to the tip. *Terminal bristles on inner side:* an apparently bare area showing the tip of a spinule from the under surface, followed by 2 more or less outwardly directed bristles and numerous recumbent bristles.

The under surface is without bristles except at the tip, the spinules beginning on the outer lateral surface and spreading to the inner surface as 2 indistinct rows just behind the tip. From the under view 3 spinules are visible near the inner surface.

Comments

P. macrophthalmus, *P. longispinosus*, and *P. emarginatus* all have somewhat similar pleopods, viz. short, robust, markedly curvate, and bearing a series of moderately elongate hairs on the inner surface. The spinulation on the under surface affords a clear distinction between *P. longispinosus* and *P. emarginatus* (see below). Existing figures of *P. macrophthalmus* (Edmondson 1954, figs. 18*e*, 18*f*) are not detailed enough for exact comparison, but no spinulation or terminal armature of any kind is shown.

Distribution

Not previously recorded from Australia, but known in the Indo-West-Pacific from the Persian Gulf and Mauritius (Alcock 1899) to Japan (Sakai 1939), New Caledonia (Milne Edwards 1873), and Hawaii (Edmondson 1954).

PORTUNUS BROCKI (de Man)

Figs. 2*G*, 3*G*; Plate 2, Fig. 3; Plates 4*G*, 5*G*

Neptunus brockii de Man, 1887*a*, pp. 328–31, pl. xiii, fig. 4.

Neptunus (*Hellenus*) *brockii* de Man. Alcock, 1899, pp. 43–4. Shen 1937, p. 111, figs. 7, 8*e*, 8*f*.

Material Examined and Illustrated

QUEENSLAND: ♂ 28 mm, fragmented, Dunk I., Family Group, pres. Nov. 1912, E. J. Banfield (Aust. Mus. Reg. No. P3211).

Description

Front.—In the present specimen with 4 very flat and indistinct lobes, the laterals the broader. (Alcock describes the front as "a simple lamina" and Shen as "undulating".)

Anterolateral teeth.—Increasing in sharpness from front to rear, the last large and directed laterally.

Carapace.—Reasonably broad (breadth slightly less than twice length). Anterolateral borders forming an arc whose centre is just behind the cardiac region. Posterior–posterolateral junction approximately right-angled. Surface with conspicuously elevated patches, whose granulation is not always distinct and which are separated by areas of fine pubescence. All those shown in Figure 1*B* are recognizable. Frontal elevations indistinct. Protogastrics a single diffuse mass. Mesogastrics in the form of an arrow pointing backwards and merging with the single metagastric. Cardiacs and postcardiacs well developed. Mesobranchials obscurely divided into three. Posterolateral area restricted, anterolateral area with broad band of granulations.

Chelipeds.—Moderately stout, granulated, and tomentose. Posterior border of arm in present specimen with 2 lobulated teeth. (According to Shen the distal one would normally be spiniform.) Anterior border of arm with 2 spines (2 or 3 according to Shen). Wrist with inner spine present, outer one reduced to a lobule. Hand with the 3 upper carinae, less conspicuous than usual, with the innermost ending in a spiniform lobule. Carina on outer surface distinct and granulated, that on the inner surface barely recognizable. Fingers short and stout.

Fifth leg.—With the normal fringing bristles.

Third maxilliped.—Extremely hirsute, with an anterolateral production of the merus.

Male abdomen.—Penultimate segment with slightly convex border, maximum breadth a little over twice that of ultimate segment. Shape very similar to that of *P. granulatus.*

First male pleopod.—Curved, stout, and bluntly ending. Just beyond the basal lobes on the inner side there is an area of closely packed short spinules. These extend right along the appendage, becoming smaller and more distantly spaced towards the tip. Inner surface bare for the proximal half, then bearing short spinules which become longer, more hair-like, and more closely packed towards the tip. The under surface of the appendage bears numerous small spinules which are in continuity with the area on the proximal portion of the outer surface. *Terminal bristles on the outer side:* minute, backwardly directed spinules commencing some distance behind the tip. *Terminal bristles on the inner side:* numerous short hairs beginning a short distance behind the tip. (Shen's figures 8*e*, 8*f* show a generally similar form of the appendage, but not the proximal area of fine spinules nor the distinction between the outer spinules and inner hairs near the tip.)

Distribution

Not previously recorded from Australia and known only from Amboina (de Man 1887*a*), the Andamans (Alcock 1899), and Singapore (Shen 1937).

PORTUNUS EMARGINATUS, sp. nov.

Figs. 2*H*, 3*H*; Plate 2, Fig. 4; Plates 4*H*, 5*H*

Material Examined and Illustrated (*Holotype*)

QUEENSLAND: ♂ 15 mm, Darnley I. (Previously identified by M. Ward as "*Xiphonectes leptocheles*? A.M.E.") (Macleay Museum.)

Description

Front.—Four flat rounded lobes, the medians very much smaller than the laterals.

Anterolateral teeth.—First large and blunt, the fourth and sixth noticeably smaller than the remainder, the ninth extremely long.

Carapace.—Extremely broad (breadth 2·4 times length), bearing very large orbits. Anterolateral borders concave anteriorly and the posterior–posterolateral junction approximately a right angle. Finely pubescent and with elevated granular areas. These consist of frontals, a large gastric mass with subregions ill defined, a single median cardiac, 3 postcardiacs, mesobranchials divided into 2, broad anterolaterals, conspicuous epibranchials, and broad posterolaterals. The posterior border is finely beaded.

Chelipeds.—Elongate, slender, and granular. Posterodistal border of the arm bearing a lobule followed by a blunt spine. Anterior border of the arm with 4 spines. Two usual wrist spines are elongate. Upper surface of hand with only 2 carinae, each ending in a conspicuous spine. The usual carinae are present on inner and outer surfaces of hand. Movable finger less grooved than normal.

Fifth leg.—Posterodistal border of merus finely serrated.

Third maxilliped.—Antero-external angle produced forwards but not laterally.

Male abdomen.—Penultimate segment with borders extremely concave and broader than long; ultimate segment rounded and about as broad as long.

First male pleopod.—Short and robust, curving smoothly but sharply to an oblique and slightly flared tip. Beyond the basal lobes on the outer surface bare to just behind the tip. Inner surface bare for the first third, from there to the end is an irregular series of hairs of which the second is extremely large and conspicuous. *Terminal bristles on the outer side:* 12 microscopic spinules in 2 rows extending almost to the tip. *Terminal bristles on the inner side:* a bare area followed by 2 backwardly directed spinules one above the other, then by a sparse row of forwardly directed hairs.

The spinules visible at the tip are part of a series beginning on the under surface approximately half-way back and becoming denser and more widespread immediately behind the tip, here passing conspicuously to the outer side but only just to the inner side.

Colour.—Dried specimen with dark patches on fingers and middle of hand of the cheliped, also dark bands on the legs and across the propodus of the fifth leg. Dark margins to the gastric regions of the carapace just above the epibranchial and round the median postcardiac area.

Comments

This species is close to *P. macrophthalmus* Rathbun and to *P. longispinosus* (Dana) in the structure of the male pleopods and in having an irregular series of anterolateral teeth. It further resembles *P. longispinosus* in having two spines on the upper surface of the hand of the cheliped, and *P. macrophthalmus* in the concavity of the lateral borders of the penultimate segment of the male abdomen. The species is distinguished by the shape of this structure (hence the specific name) and by the details of male pleopod structure.

PORTUNUS GRANULATUS (Milne Edwards, H.

Figs. 2*I*, 3*I*; Plate 3, Fig. 1; Plates 4*I*, 5*I*

Lupea granulata Milne Edwards, H., 1834, p. 454.

Achelous granulatus (Milne Edwards, H.). Milne Edwards, A., 1861, p. 344.

Neptunus (*Achelous*) *granulatus* (Milne Edwards, H.). Ortmann, 1893, p. 72. Alcock, 1899, pp. 45–6 (lit. and synon.). Boone, 1934, pp. 61–2, pl. xx. Sakai, 1939, p. 397, pl. lxxxi, fig. 3.

Portunus (*Achelous*) *granulatus* (Milne Edwards, H.). Rathbun, 1906, p. 871, pl. xli, fig. 6; 1911, p. 205, pl. xv, fig. 10. Balss, 1938, p. 31. Edmondson, 1954, p. 239.

Material Examined

19 ♂♂ (21–26 mm); 4 ♀♀ (11–23 mm).

QUEENSLAND: Darnley I., Morris I. (Claremont Group), Murray I., Low Isles, Cairns, Port Denison, Heron I., North West I. NEW SOUTH WALES: Port Jackson.

Recorded habitats: Dredged, 5–7 fm.

Material illustrated: ♂ 26 mm, Heron I., Aug. 1948, coll. I. M. and M. J. Mackerras (Zool. Dept. Univ. Qld.).

Description

Front.—Two broad, reasonably sharp lateral lobes and a central mass consisting of 2 lobes which fuse medianly and on a lower plane. Depending upon the aspect, this central area could be described as a single lobe, 2 lobes, or even 3.

Anterolateral teeth.—Approximately of equal size, the first the broadest, the fourth usually the smallest, the last slightly the most protruding.

Carapace.—Narrow (breadth *c.* 1½ times length). Anterolateral borders form a narrow arc whose centre lies a little forward of the cardiac region. Posterior–posterolateral junction rounded. Surface covered with close-packed granulated areas with a fine pubescence among the granules. All the areas indicated in Figure 1*B* are present excepting the frontals and orbitals, but are not very clearly recognizable in the more hirsute specimens. Protogastrics each as 2 confluent patches; meso- and metagastrics fused, but the latter with a prominent anterior margin almost forming a ridge; cardiac almost divided in the mid line; postcardiacs very prominent; anterolaterals well developed and sharply marked off from an unnamed area just behind, which in turn merges with an indistinctly subdivided epibranchial and mesobranchial area; posterolateral area extensive.

Chelipeds.—Elongate, granular, and hirsute, except on under surface which is polished and pitted. Two spines on the posterior border of the arm, one two-thirds of the way along and one distal. Anterior border of arm with spines set among spiniform granules. The spines become smaller proximally and merge into tubercles, approximately 5 spines and up to 2 tubercles being present. Wrist with the 2 usual spines. Hand with 3 usual upper carinae, the innermost being much the best developed and the only one terminating in a spine. Outer carinae very well developed, inner one not recognizable amongst the lines of tubercles.

Fifth leg.—With the usual fringing hairs.

Third maxilliped.—Antero-external angle of merus acutely produced in a lateral direction.

Male abdomen.—Penultimate segment with slightly convex borders, maximum breadth a little over twice that of ultimate segment. Shape very similar to that of *P. brocki*. (The ultimate segment in the present specimens is longer than figured by Sakai (1939, text fig. 86). The penultimate segment as figured by Gordon (1938, fig. 6*b*) has much less convergent sides.)

First male pleopod.—Short, stout, with an undulating outer side and widely flared tip. Continuing from the basal lobes on both outer and inner sides there is a row of bipinnate hairs which extend about two-thirds of the way up the appendage. No terminal armature is visible in profile view, but on the under surface there are small backwardly directed spinules which begin about one-fourth of the way down the appendage and extend to form numerous irregular rows. These terminate on the level of the larger of the flared lips and extend across the entire under surface. Within the lips the forwardly directed surface of the larger lip bears a series of fine, small, hair-like bristles, of which approximately 9 are visible in profile view.

Comments

The first male pleopod has been figured by Gordon (1938, fig. 5*e*) with the flared lip imperfectly shown, and by Edmondson (1954, fig. 16*b*), whose figure is barely recognizable. The pleopod is quite unlike that of any other species of *Portunus* so far figured, and in the form of the tip shows resemblances to the genus *Charybdis* (see Stephenson, Hudson, and Campbell 1957, fig. 3). However, it possesses a much wider flare, and is somewhat reminiscent of *Thalamita sexlobata* and *T. sima* (see Stephenson and Hudson 1957, figs. 3*b*, 3*c*).

Distribution

Published and present records within Australia are from Queensland (Calman 1900; Boone 1934), New South Wales (present records), West Australia (Rathbun 1924), and North Australia (Henderson 1893).

Outside Australia extending from Mauritius, Madagascar, and the Red Sea to Hawaii, Samoa, and Fiji (fide Sakai 1939).

PORTUNUS GLADIATOR Fabricius

Figs. 2*J*, 3*J*; Plate 3, Fig. 2; Plates 4*J*, 5*J*

Portunus gladiator Fabricius, 1798, p. 368.

Cancer menestho Herbst, 1803, p. 34, pl. lv, fig. 3.

Portunus (*Amphitrite*) *gladiator* Fabricius. De Haan, 1833, p. 39, pl. i, fig. 5.

Lupea gladiator (Fabricius). Milne Edwards, H., 1834, p. 456.

Neptunus gladiator (Fabricius). Milne Edwards, A,, 1861, pp. 330, 339. De Man, 1897*b*, pp. 69–70.

Neptunus (*Amphitrite*) *gladiator* (Fabricius). Alcock, 1899, pp. 35–6 (lit. and synon.). Balss, 1922, p. 107. Shen, 1937, pp. 101–3, fig. 2. Sakai, 1939, pp. 390–1, pl. xlvii, fig. 3.

non *Portunus* (*Amphitrite*) *gladiator* de Haan, 1833, p. 65, pl. xviii, fig. 1 (= *P. orbitosinus* Rathbun).

Material Examined

WESTERN AUSTRALIA: ♂ 28 mm, Ninety-Mile Beach between Cape Jaubert and Wallal, dredged 5 fm, Sept. 1929 (Aust. Mus. Reg. No. P12602). ♀ 44 mm, dredged between C. Bossut and Broome, 5 fm, 11.ix.1929 (Aust. Mus. Reg. No. P12596).

Material illustrated.—Ninety-Mile Beach specimen.

Description

Front.—Four-lobed, the medians acute, the laterals right-angled and much broader.

Anterolateral teeth.—First stout and blunt, then increasing in size and sharpness to the eighth, the ninth a long spine directed outwards.

Carapace.—Moderately broad (breadth *c.* 1·8 times length). Anterolateral borders form an arc whose centre lies behind the cardiac region. Posterior–posterolateral junction rounded and with a right-angled projection on a lower plane. Surface covered with widely spaced, very conspicuously granular areas, these being separated by regions with a dense pubescence. All the areas shown in Figure 1*B* are present except that the frontals and orbitals are sometimes absent. Protogastrics almost subdivided into 2, the posterior portion merging with the transverse mesogastric, giving a semblance to a granulated ridge; the anterior portion of the metagastrics gives a similar appearance; ill-defined separation between the two halves of the cardiac region; 3 distinct postcardiacs; anterolaterals with a more or less discrete patch opposite each tooth; epibranchials distinct; each mesobranchial consisting of 3 or 4 distinct patches; posterolaterals small; posterior border of carapace finely beaded.

Chelipeds.—Stout, pubescent, and granular, with squamiform markings on under surface. Posterodistal border of arm with 2 large spines, anterior border with 4. Wrist with the 2 usual spines; the outer being more than usually developed. Three usual carinae on the upper surface of the hand, of which only the innermost ends in a spine. Carina on outer surface of hand very distinct, that on inner surface barely recognizable.

Fifth leg.—Posterodistal border of merus serrated, the last 1 or 2 serrations being spiniform.

Third maxilliped.—Antero-external angle of merus produced laterally.

Male abdomen.—⊥-shaped, penultimate segment less than twice as long as broad, ultimate segment twice as long as broad. (The male abdomen in the present specimen is longer and narrower than figured by Sakai (1939, text fig. 5*a*) or by Shen (1937, fig. 2*b*).)

First male pleopod.—Short, only slightly curved, and regularly tapering to a rounded end. Beyond the basal lobes on the outer surface backwardly directed spinules begin about half-way up the appendage as a fairly dense row which becomes sparser and continues to just behind the tip. Inner surface bare until the distal third, where backwardly directed, sparsely arranged, small spines (some 6 in number) continue to just behind the tip. Tip itself bare in profile view apart from the above bristles. On the upper surface backwardly directed spinules begin about one-third of the way up the appendage and continue mostly nearer the inner edge but eventually give a sparse cover to the whole under surface in the region behind the tip.

Comments

The ♀ 44 mm, P12596, is abnormal in having only 8 teeth on the right anterolateral border, the fourth of those normally present being represented only by a small spine distinctly median to the carapace margin.

Distribution

Although Sakai (1939) lists Queensland in his distributional data, the nearest acceptable published record the present authors have obtained lies nearer New Guinea (Miers 1886).

Known from Mauritius to Japan (Sakai 1939).

PORTUNUS RUBROMARGINATUS (Lanchester)

Figs. 2*K*, 3*K*; Plate 3, Fig. 3; Plates 4*K*, 5*K*

Achelous rubromarginatus Lanchester, 1900, pp. 746–7, pl. 46, fig. 8.
Neptunus (*Amphitrite*) *rubromarginatus* (Lanchester). Shen, 1937, p. 104.

Material Examined

30 ♂♂ (15–54 mm); 22 ♀♀ (13–50 mm). Ovigerous ♀ 38 mm from Aug.–Sept.

QUEENSLAND: Albany Passage, Albany I., Palm I., Port Denison, Mackay, Prudhoe I., Scawfell I., Port Curtis, Moreton Bay (Dunwich, Woody Point). NEW SOUTH WALES: Port Jackson. WESTERN AUSTRALIA: Cygnet Bay, C. Jaubert, Wallal, Marat I., Exmouth Gulf.

Recorded habitats.—Trawled, sandy mud, 3–12 fm.

Material illustrated.—♂ 51 mm, 3½ miles S. Woody Point pier, 19.x.1952, E.M.G. (Zool. Dept. Univ. Qld.).

Description

Front.—Four-lobed, the 2 medians distinct and acute, the laterals right-angled and much broader.

Anterolateral teeth.—Approximately of equal size, the first broad and blunt, the next 7 subequal, the last distinctly the broadest and most protruding, and directed slightly forwards.

Carapace.—In most specimens narrow (breadth *c.* 1½ times length). In some smaller specimens moderately broad (just less than twice length). Anterolateral borders form a reasonably narrow arc whose centre lies just behind the cardiac region. Posterior–posterolateral junction rounded and with a rounded projection on a lower plane. Surface covered with widely spaced very conspicuously granulated areas, these being separated by regions with a dense pubescence. All the areas shown in Figure 1*B* are present. Frontals lie a little behind the elevated border; the orbitals lie on this border; protogastrics subdivided; mesogastrics subdivided into central area and a pair of laterals; a pair of metagastrics; a pair of cardiacs; 3 distinct postcardiacs; anterolaterals with a more or less discrete patch opposite each tooth; epibranchial distinct; mesobranchial consisting of 4 discrete patches; posterolaterals small; posterior border of carapace finely beaded.

Chelipeds.—Pubescent and with squamiform granulation. Posterodistal border of arm with a single spine, just proximal to which a beaded carina reaches the lower margin. Anterior border of the arm with 3–5 spines. Wrist with the 2 usual spines, each marking the end of a beaded carina. Upper surface of hand with the 3 usual carinae, each granular, but only the innermost ending in a spine. Carina on outer surface distinct and granular, that on the inner surface barely recognizable.

Fifth leg.—Posterodistal border of merus very finely serrated.

Third maxilliped.—Antero-external angle of merus produced laterally.

Male abdomen.—Proximal end of ultimate segment much narrower than distal end of penultimate, giving a step-like junction; both segments with straight sides.

First male pleopod.—Elongate, slightly curved, most of the taper in the proximal half and then with a gentle taper to a slightly indented membranous tip. Beyond the basal lobes about half-way up the appendage on the outer surface there is a dense cluster of backwardly directed spinules, these thinning out but continuing almost to the tip and in the course of doing so becoming slightly forwardly directed. The inner surface is bare for the proximal three-fourths and thereafter there is a row of microscopic bristles. These are sparsely arranged, at right angles to the appendage, and increase in density towards the tip, terminating just behind it. *Terminal bristles on the outer side* are absent; *on the inner side*, slightly back from the tip, there may be either none or very few spinules before the row of microscopic bristles begins. These spinules are part of a series which leads from the dense cluster on the outer surface to give a sparse covering to the ventral surface, this extending almost to the tip, and near the tip crossing to, or almost to, the inner surface.

Colour.—After moderately prolonged alcohol preservation usually the spines on the anterior border of the arm and on the anterolateral border are a fleshy pink.

Distribution

The only previous records are from the South China Sea, Hong Kong, and the Malay Archipelago (fide Shen 1937) but evidently the species is moderately common in the northern half of Australia.

PORTUNUS ORBITOSINUS Rathbun

Figs. 2*L*, 3*L*; Plate 3, Fig. 4; Plates 4*L*, 5*L*

Portunus (*Amphitrite*) *gladiator* de Haan 1833, only p. 65, pl. xviii, fig. 1.* (Non *Portunus gladiator* Fabricius 1798.)

Portunus (*Achelous*) *orbitosinus* Rathbun, 1911, p. 205, pl. 15, fig. 11.

Neptunus (*Achelous*) *orbitosinus* (Rathbun). Gordon, 1938, pp. 182–5, figs. 5*a*–5*g*, 6*c*, 6*d*.

Neptunus (*Achelous*) *orbitospinis* (Rathbun). Sakai, 1939, p. 396, pl. lxxxi, fig. 2.

* De Haan (1833), p. 39, pl. i, fig. 5 is true *Portunus gladiator* Fabricius.

Material Examined and Illustrated

QUEENSLAND: ♂ 33 mm, Mapoon, pres. Aug. 1903, C. Hedley (Aust. Mus. Reg. No. G4230).

Description (based on a single specimen)

Front.—Two protruding lateral lobes and a central mass consisting of 2 lobes which fuse medianly and on a lower plane. These lobes are larger than in *P. granulatus*. Depending on the aspect, this central area could be described as a single lobe, 2 lobes, or even 3.

Anterolateral teeth.—Nine in number, of approximately equal size and all sharp, the first the broadest, the second the smallest, the last slightly the most protruding.

Carapace.—Narrow (breadth *c.* 1½ times length). Anterolateral borders form a narrow arc whose centre lies in the cardiac region. Posterior–posterolateral junction rounded. Surface covered with widely spaced, very conspicuous, granulated areas, these being separated by regions with a dense pubescence. All the areas shown in Figure 1*B* are present. Frontals and orbitals lie a little behind the elevated fronto-orbital ledge; protogastrics almost subdivided; meso- and metagastrics confluent; one pair of cardiacs; postcardiacs very distinct; anterolaterals as a series of patches; epibranchials a diffuse band curving far forwards; mesobranchial 4 distinct patches; posterolaterals well developed; posterior border of carapace beaded.

Chelipeds.—Granular and with a dense pubescence, except on the under surface, which bears squamiform markings. Arm with posterior border bearing 2 spines, the proximal (the sharper) lying about two-thirds of the way along and marking the end of a granular carina. The spines on the anterior border become smaller proximally, 4 are present on the right chela and 4 plus 2 stout spiniform tubercles on the left. Wrist with 2 usual spines. Upper surface of hand with 3 usual carinae, all granular, and only the inner ending in a spine. Carina on outer surface distinct, on inner surface just recognizable as a row of slightly more prominent tubercles.

Fifth leg.—Posterodistal border of merus with small serrations.

Third maxilliped.—Antero-external angle of merus produced acutely in a lateral direction.

Male abdomen.—Penultimate segment swollen, i.e. with extremely convex borders, maximum breadth nearly 3 times breadth of ultimate segment. (In Sakai's (1939) text figure 8*a*, the ultimate segment is less pointed than in the present specimen. In Gordon's (1938) figure 6*d*, the sides of the penultimate segment are less smoothly curved.)

First male pleopod.—Reasonably long, curving smoothly to a narrow tip, which is thinned out into a spoon-shaped membrane. No ornamentation on either side from the basal lobes until near the tip. The outer side of the tip with no armature and the inner side with 3 or 4 microscopic spinules. Three microscopic hairs are present on the upper surface of the membrane and a scattered series of *c.* 10 spinules on the under surface of the appendage, the most distal reaching just to the membrane.

Comments

Gordon noted some differences between a specimen from Singapore and cotypes of the present species, and suspected the existence of an undescribed species for which she suggested the name *Neptunus octodentata.* The present work, which is the most extensive to date on pleopods in this genus, confirms her suspicion. It is inconceivable that the variation in pleopod structure within *P. orbitosinus* could encompass the structures she figured (figs. 4*c*, 4*c*^{1}). Evidently some variation occurs within this species, and Gordon's figure 5*f* shows hairs or bristles on the outside of one appendage which are not present upon two others or upon the specimen here examined.

Distribution

Seychelles (Rathbun 1911) to Japan (Sakai 1939). Not previously recorded from Australia.

PORTUNUS GRACILIMANUS (Stimpson)

Figs. 2*M*, 3*M*; Plate 4, Fig. 1; Plates 4*M*, 5*M*

Amphitrite gracilimanus Stimpson, 1858, p. 38; 1907, p. 77, pl. x, fig. 3.

Achelous whitei Milne Edwards, A., 1861, pp. 336, 343, pl. xxxi, fig. 6. Lanchester, 1900, p. 746.

Neptunus (*Lupocycloporus*) *whitei* (Milne Edwards, A.). Alcock, 1899, pp. 44–5. Laurie, 1906, p. 416.

Portunus (*Lupocycloporus*) *innominatus* Rathbun, 1909, p. 114.

Neptunus (*Lupocycloporus*) *gracilimanus* (Stimpson). Alcock, 1899, p. 45. Balss, 1922, p. 108. Chopra, 1935, pp. 481–2. Shen, 1937, pp. 113–4, fig. 9.

Material Examined

4 ♂♂ (19–40 mm); 2 ♀♀ (16 and 17 mm).

QUEENSLAND: Albany Passage (Cape York), Townsville, Port Curtis.

Recorded habitats.—Dredged 9 fm.

Material illustrated.—♂ 40 mm, Magnetic I., Feb.–March 1953, R. K. Bryson (Zool. Dept. Univ. Qld.).

Description

Front.—Four teeth, of which the lateral pair are slightly broader and the median pair slightly the more projecting.

Anterolateral teeth.—After the first, increasing in length and sharpness, the last approximately twice the length of the others.

Carapace.—Only moderately broad (breadth *c.* 1¾ times length). Anterolateral borders forming an arc whose centre lies behind the cardiac region. Posterior–posterolateral junction rounded. Surface covered with conspicuous ridges, between which there is a fine dense pubescence. All the ridges shown in Fig. 1*A* are present. Protogastrics are interrupted in the mid line while the meso- and metagastrics are continuous. Epibranchial forks obscurely near its inner termination. The anterior mesobranchial and the cardiacs are actually the discrete anterior borders of granular patches. Similar but less well-defined patches occur in the frontal, orbital, anterolateral, and median postcardiac regions (see Fig. 1*B*). Posterior border of carapace beaded.

Chelipeds.—Very elongate, the wrist and hand much more slender than the arm; with numerous squamiform granules and a fine pubescence. Posterior border of the arm with 2 sharp spines, one about two-thirds of the way along, marking the end of a conspicuous granular carina, the other terminal. Wrist with the 2 usual spines, both elongate. Hand with the 3 usual upper carinae, the 2 innermost terminating in long spines. The spine at the wrist articulation is also elongate and sharp. Granular, but somewhat rounded carinae on both inner and outer surfaces of the hand. Fingers slender, compressed, ending very acutely, with tips bent slightly outwards.

Fifth leg.—Posterodistal border of the merus ending in a sharp spine.

Third maxilliped.—Hirsute, antero-external angle of merus slightly produced laterally.

Male abdomen.—Ultimate and penultimate segments with straight sides, except for the slightly rounded tip of the former.

First male pleopod.—Short, very stout, sharply curved, narrowly tapering at the extreme tip. Beyond the basal lobes on the outer side bare to the tip, except that the point only of an occasional spinule from the upper surface may be seen. Inner surface beyond the basal lobes in the proximal third bears a sparsely arranged row of forwardly directed elongate hairs. Near the tip 9 backwardly directed short stout spines.

The tip itself tapers abruptly at the extreme end and behind this the conspicuous ornamentation is on the *upper* surface. This consists of (1) a moderately dense area of backwardly directed spinules on the outer half of the upper surface, these extending almost to the tip, where they become very small; and (2) a shorter patch of much larger backwardly directed spines on the inner half of the upper surface. Some two dozen spines are present, the uppermost being the largest, the lowermost showing in lateral view, the most distal being very small and not extending into the sharply tapered area.

Comments

Rathbun (1907) has shown that *P. whitei* (Milne Edwards 1861) is synonymous with *Amphitrite gracilimanus* Stimpson, 1858, and the present specimens belong to this species. It is less certain whether *Neptunus gracilimanus* Alcock non Stimpson (= *P. innominatus* Rathbun) is distinct from the above or synonymous with it. The position is complicated by Chopra's (1935, p. 481, footnote) statement: "I have also examined the specimens that Alcock called *gracilimanus*, and am of the opinion that they cannot be referred to any of the known species of *Neptunus* (*Lupocycloporus*)". Shen (1937) considers that *N. gracilimanus* Alcock is a synonym of *N. whitei* Alcock and in erecting his new species *N. minutus* makes no detailed comparison with the former, i.e. *Portunus innominatus* Rathbun. A detailed re-examination of the specimens of this group from extra-Australian sources is necessary before the validity and affinities of *P. innominatus* in particular can be determined. Therefore the above synonymy, with some hesitation, follows Shen (1937).

Distribution

Previously recorded from Gladstone, Queensland, by Grant and McCulloch (1907).

Distribution outside Australia from the Andamans, east coast of India, Hong Kong, and Malaya, to New Guinea (Alcock 1899; Chopra 1935; Shen 1937).

VII. Discussion

(*a*) *Subgenera*

The outstanding problem in this genus, as indicated in Section II, concerns the distinctness of the subgenera, and here knowledge of the structure of the first pleopods of males is helpful. Of the few studies which have been made in the past, several are insufficiently detailed, and even with the present detailed work, in a majority of species these structures have not yet been investigated. A consideration of the minority does, however, give helpful indications.

The first male pleopods of *P. pelagicus. P. sanguinolentus*, and *P. pubescens* are all elongate, smoothly curving, and practically parallel-sided structures whose terminal armature consists of laterally placed, robust, backwardly directed spines. The resemblances between the three species are close, and there are no other species approaching them at all closely in pleopod structure. On this basis, *P. pubescens* would clearly belong to the subgenus *Portunus* in spite of its carapace not having quite the characteristic breadth. The subgenus itself would appear to be worth maintaining in existence.

Two other Australian species stand apart on the basis of pleopod structure, but as individual species. They are *P. gracilimanus* and *P. granulatus*. The former is unique in possessing an appendage which is sharply curved, extremely robust, and bears robust backwardly directed spines on the upper surface. Allied with the general facies and especially the pronounced slenderness of the arm, this species is sufficiently distinctive to validate the continued application of the subgenus *Lupocycloporus*.

The other species (*P. granulatus*) is equally distinctive, the pleopod being very broad, with bipinnate hairs proximally on its lateral borders and a flared tip. It is also distinctive amongst the Australian species by the narrowness of its carapace. Together with *P. orbicularis*, it was placed in Alcock's subgenus *Achelous*, now Ward's *Cycloachelous*. Unfortunately, in *P. orbicularis*, according to Edmondson's figures (1954, figs. 16*d*, 16*e*), the structure of the male pleopod is very different from *P. granulatus*. It should be noted that Edmondson's figure of *P. granulatus* (fig. 16*b*) bears little resemblance to actuality. However, his figures of *P. orbicularis* (16*d*, 16*e*), while needing refiguring, could not possibly be from an animal bearing a pleopod resembling that of *P. granulatus*. It seems probable (1) that the subgenus *Cycloachelous* is not a homogeneous group and (2) that *P. granulatus* is sufficiently distinctive from all other species in the genus to be placed in a separate subgenus.

P. gladiator and *P. rubromarginatus* have elongate, moderately straight pleopods, whose upper surfaces near the tip are practically bare and whose lower surfaces bear minute spinules. *P. orbitosinus* has comparable terminal armature, but the curved form of the appendage gives it a very different general appearance. These three species all belong to Alcock's subgenus *Amphitrite*, correctly *Monomia*, and give qualified support to the reality of this grouping. Against this, the terminal armature of *P. argentatus* (in the same "subgenus"), as figured by Edmondson (1954, figs. 14*c*, 14*d*), is apparently quite different.

The remaining Australian species all belong to Alcock's subgenus *Hellenus*, correctly *Xiphonectes*, and in all cases the pleopods are curved in a somewhat similar fashion, usually to an acute tip. This resemblance, which would be difficult to define precisely, would not apply to *N. octodentata* as figured by Gordon (1938, figs. 4*c*, 4*c*^{1}).

Within the species of *Xiphonectes*, affinities in pleopod structure can be distinguished between *P. emarginatus* and *P. longispinosus*. In both cases the pleopods are stout distally and bear stout subterminal bristles on the inner side. Apparently the following species, as judged by published figures, also show these features: *P. macrophthalmus*, *P. pulchricristatus*, and *P. spinipes*. This is a tolerably natural grouping, judged on the basis of general facies, with *P. emarginatus*, *P. longispinosus*, and *P. macrophthalmus* being especially close. The pleopod of *P. nipponensis*, as figured by Sakai (1939, text fig. 7), also shows affinities to this group.

The remaining Australian species (*P. hastatoides*, *P. tenuipes*, and *P. brocki*) lie outside this grouping and show no special affinities one with another.

In conclusion it appears:

(i) that *P. pelagicus*, *P. sanguinolentus*, and *P. pubescens* have a close affinity with one another;

(ii) that *P. gracilimanus* is distinctly apart from the remainder;

(iii) that the remaining Australian species, whose segregation into different subgenera on the basis of general facies is difficult, are an equally confused assemblage on the basis of structure of the male pleopods.

(*b*) *Possible Origin of the Genus*

There seems to be general agreement on the probable origin of most of the Portunids from a genus such as *Carcinus* Leach, 1814, and this will be commented upon in a later paper of this series. Three main structural developments are required to convert a walking, crevice-dwelling crab like *Carcinus* into a swimming and shallowly burrowing crab like *Portunus pelagicus*. These are first a flattening of the fifth legs, secondly a broadening of the carapace, and thirdly an increase in size.

Flattening of the fifth legs occurs to some extent in genera close to *Carcinus*, and can probably be regarded as the initial development. The highly successful genus *Thalamita* Latreille, 1829, which has already been treated in this series (Stephenson and Hudson 1957), can probably be regarded as the culmination of an evolutionary development on the general line towards *Portunus*, but which has involved little more—of an obvious nature—than the legs. From a broadly functional viewpoint *Thalamita* spp. are not swimming crabs; they usually walk upon their second to fourth legs and assist their walking by flipping actions of the fifth legs.

The most obvious significance of a broadening of the carapace would appear to be in effecting some degree of streamlining with respect to lateral motion (see Schäfer 1954). On this basis the groups which obtain maximum "flipping" propulsion from their fifth legs can be expected to be the broadest. Broadening of the carapace involves elongation of both the anterolateral and posterolateral borders. Since the former bears teeth, one of two things would result—either the same number of larger teeth, or a greater number of teeth. The latter appears to have happened, and from five anterolateral teeth in *Carcinus* and *Thalamita* (most species), the evolutionary trend would appear to be six teeth in *Charybdis* de Haan, 1833 (see Stephenson, Hudson, and Campbell 1957), and nine in *Portunus* (most species) and *Scylla* de Haan, 1833.

The critical place of *Charybdis* in this progression should be noted, especially since within the genus the teeth vary in number. Some species possess five well-developed teeth and one smaller tooth (these approach *Thalamita*), others have six well-developed teeth, and yet others have five well-developed teeth with three small teeth. These last approach *Portunus*, especially such species as *P. longispinosus*, *P. macrophthalmus*, and *P. emarginatus*, which normally possess irregular anterolateral teeth, and also *P. gladiator*, which occasionally shows this phenomenon. The fact that in *Charybdis* the carapace is broader in juveniles than in adults (at least in some species, e.g. *C. helleri* (A. Milne Edwards 1867), see Stephenson, Hudson, and Campbell 1957, text fig. 1*C*, 1*D*) shows that possibly swimming is more characteristically a juvenile activity. On this basis *Charybdis* as a whole may have come from swimming ancestors and thus be secondarily demersal.

In adults of *Charybdis* swimming seems to be an infrequent phenomenon and regular swimming habits, upon which the popular name for the family depends, are only seen conspicuously (amongst the Australian adult representatives at least) in the genus *Portunus*. Once free swimming has been attained many ecological restrictions will be removed. Distribution can be extended by the adults under their own efforts, and possibly this explains the successful establishment of *P. pelagicus* in the Mediterranean and the reported establishment of *P. sanguinolentus*. Dependence upon crevices and the under-stone habitat can be expected to lessen, and with this the necessity for fitting into such habitats. In other words, different factors are likely to control the overall size. Possibly large size is an advantage in reducing the number of predators which could make successful attacks; possibly it increases swimming efficiency. All that can be stated is that certain species of *Portunus* are almost the largest and most abundant of the Australian crabs. To this they owe their economic importance.

(*c*) *Possible Evolution within the Genus*

If the above arguments are sound, the most primitive members of the genus will be those with least broadening of the carapace. Three distinct units have roughly equal claim to primitiveness on this basis. These are:

(1) *P. pubescens*; the carapace ridges and the "set" of the anterolateral teeth are typically *Charybdis*-like, while the general carapace shape shows considerable resemblances to certain species of *Charybdis*, e.g. *C. helleri* (A. Milne Edwards 1867). Of the Australian species, *P. pubescens* also appears closest to *Scylla*. Against this, the male pleopods do not greatly resemble the *Charybdis* form as previously described in this series (Stephenson, Hudson, and Campbell 1957).

From something not too different from *P. pubescens*, *P. pelagicus* and *P. sanguinolentus* could have evolved.

(2) The "*Achelous*" group, comprising *P. granulatus*, *P. rubromarginatus*, and *P. orbitosinus*. Here the carapace is at its longest and has the same general shape as certain species of *Charybdis*, e.g. adult *C. callianassa* (Herbst 1789). However, the carapace bears granular patches, as against the transverse ridges of *Charybdis*. While the male pleopods vary from one species to another, in the case of *P. granulatus*, at least, there is an approximation to the *Charybdis* form of male pleopod.

The "*Achelous*" group merges with the "*Hellenus*" group, and the important "advance" of the latter is a broadening of the carapace. This affects the ninth anterolateral tooth in a much more exclusive fashion than in the cases of *P. pelagicus* and

P. sanguinolentus, with a resultant tendency for concavity in the anterolateral borders.

On this basis it would appear that carapace broadening has happened in two different ways in two different subgroups of the genus, in other words that this is a case of parallel evolution.

(3) *P. gracilimanus* possesses a carapace broader than the majority of adult *Charybdis* species, but resembles that of juveniles (e.g. *C. callianassa*, Stephenson, Hudson, and Campbell 1957, text fig. 1*C*). It also bears *Charybdis*-like ridges on the carapace.

This species is almost as different from a generalized *Portunus* as is the genus *Scylla*, both in male pleopod structure and in the form of the chelipeds. The cheliped development, which is towards attenuation, is the reverse of that in *Scylla*, and possibly this species has an equal right to be placed in a separate genus.

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Corrigendum

VOLUME 9, NUMBER 4, PAGES 569–657

"The Family Triphoridae (Mollusca) from Northern Australia; also Triphoridae from Christmas Island (Indian Ocean)"

By C. F. Laseron

In Section V of this paper some textual matter was transposed. The descriptions of *Aclophora islandica*, *A. alveata*, *A. albozonata*, Genus *Tetraphora*, *T. mapoonensis*, and *T. borealis* (pp. 623–6) should follow after *Aclophora kerslakei*, p. 631. The second paragraph "Remarks" printed under *Opimaphora metellona* (p. 623) belongs under *Aclophora kerslakei*.

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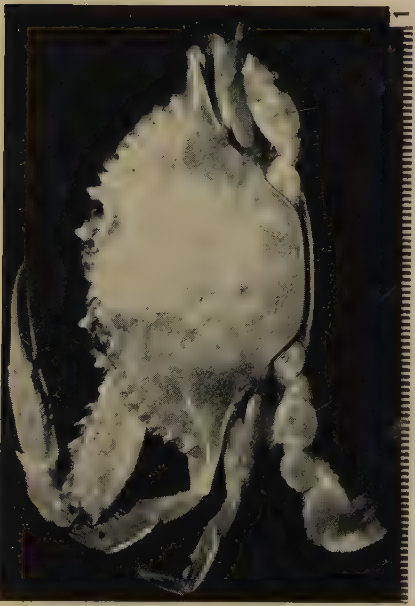

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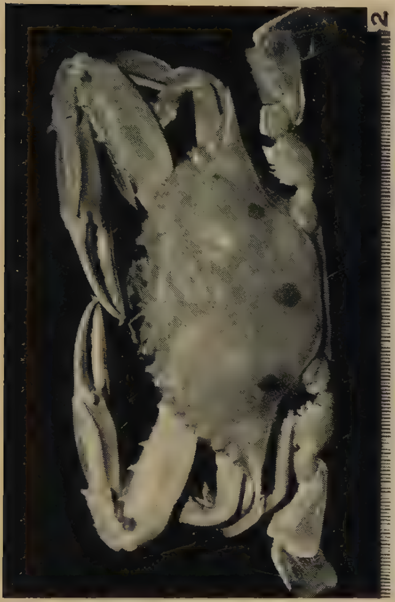

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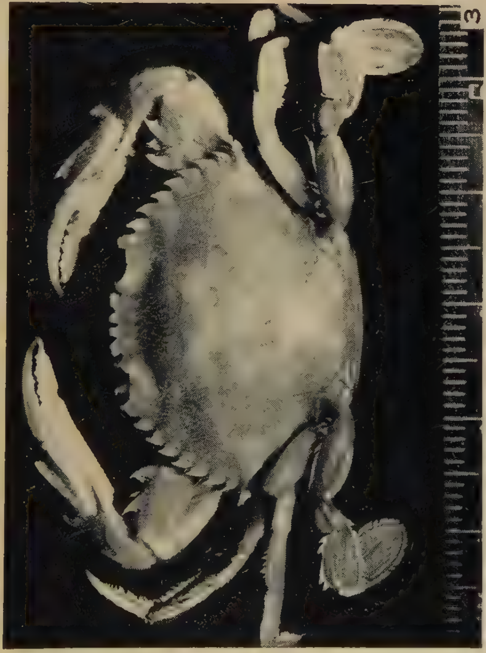

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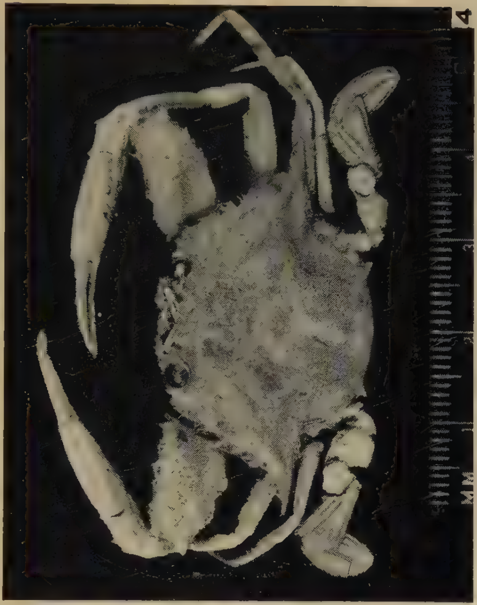
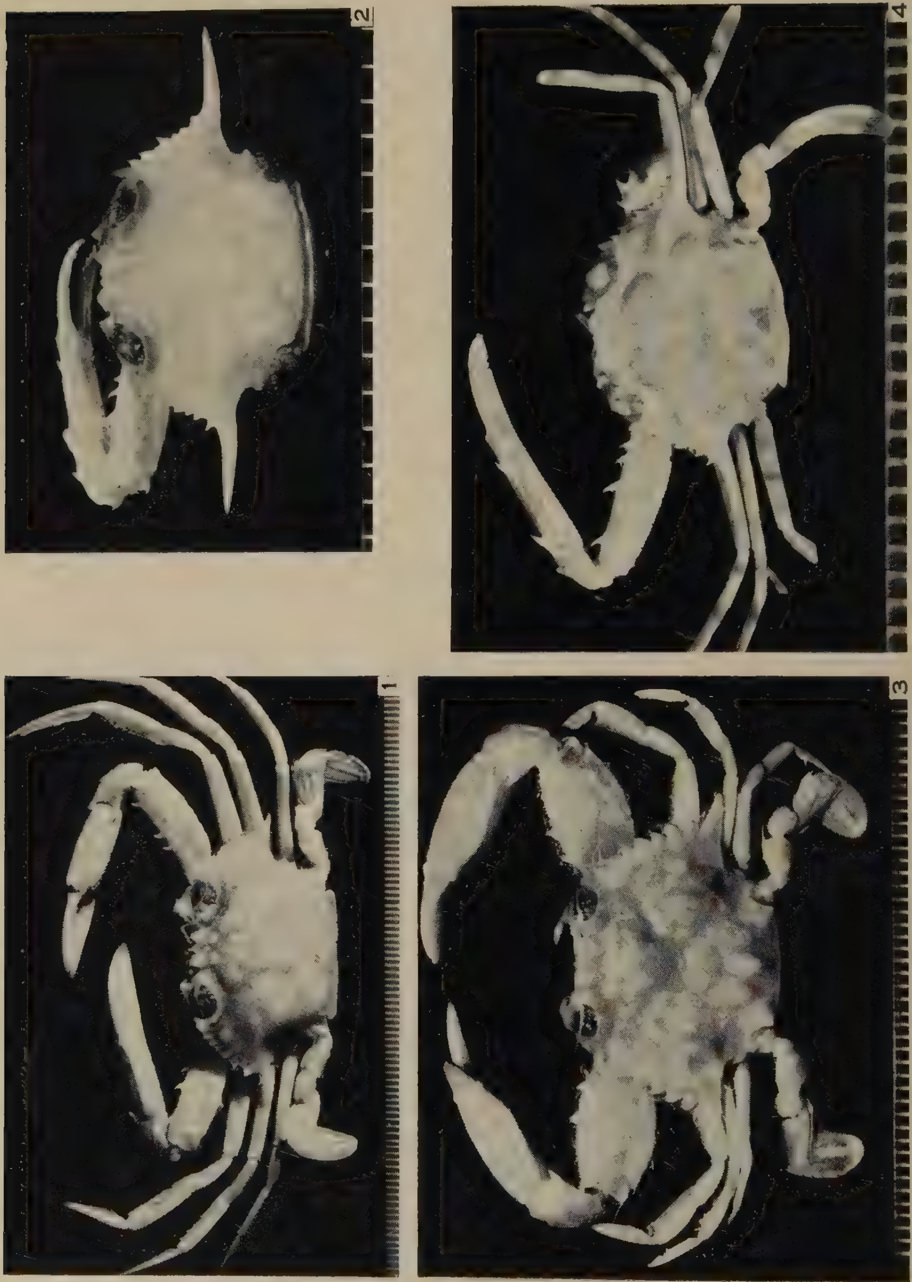


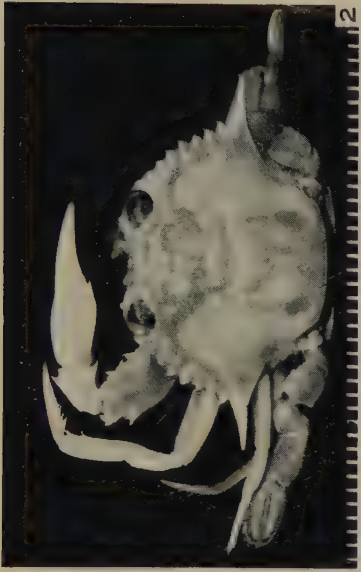
Dorsal views of *Portunus* spp. Scale divisions, 1 mm. Fig. 1. *P. pelagicus*. Fig. 2.—*P. sanguinolentus*. Fig. 3.—*P. pubescens*. Fig. 4.—*P. hastatoides*.

AUSTRALIAN PORTUNIDS. III



Dorsal views of *Portunus* spp. Scale divisions. 1 mm. Fig. 1.—*P. tenuipes*. Fig. 2.—*P. longispinosus*. Fig. 3.—*P. brocki*. Fig. 4.—*P. emarginatus*.

AUSTRALIAN PORTUNIDS. III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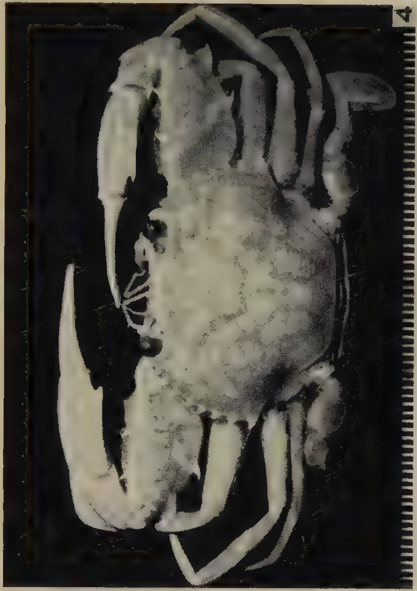
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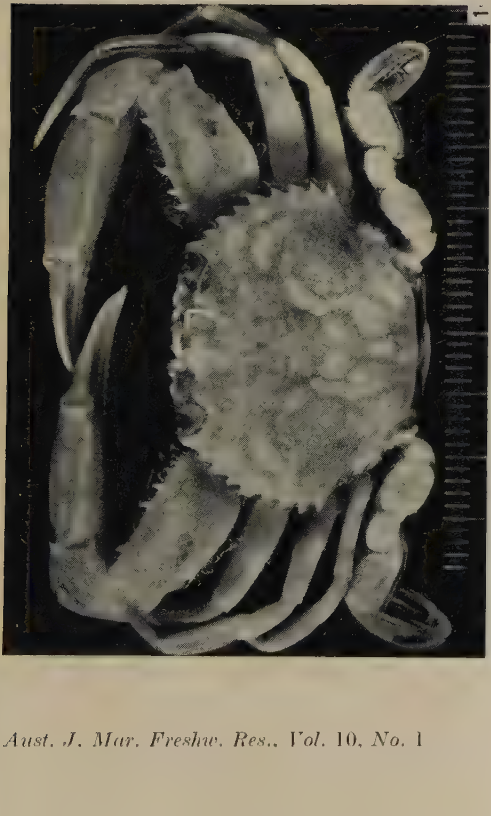
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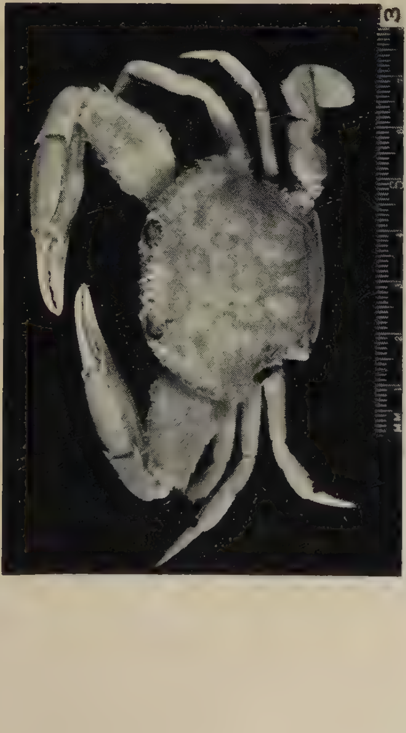
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Dorsal views of *Portunus* spp. Scale divisions, 1 mm. Fig. 1.—*P. granulatus*. Fig. 2.—*P. gladiator*. Fig. 3.—*P. rubromarginatus*. Fig. 4.—*P. orbitosinus*.

AUSTRALIAN PORTUNIDS. III

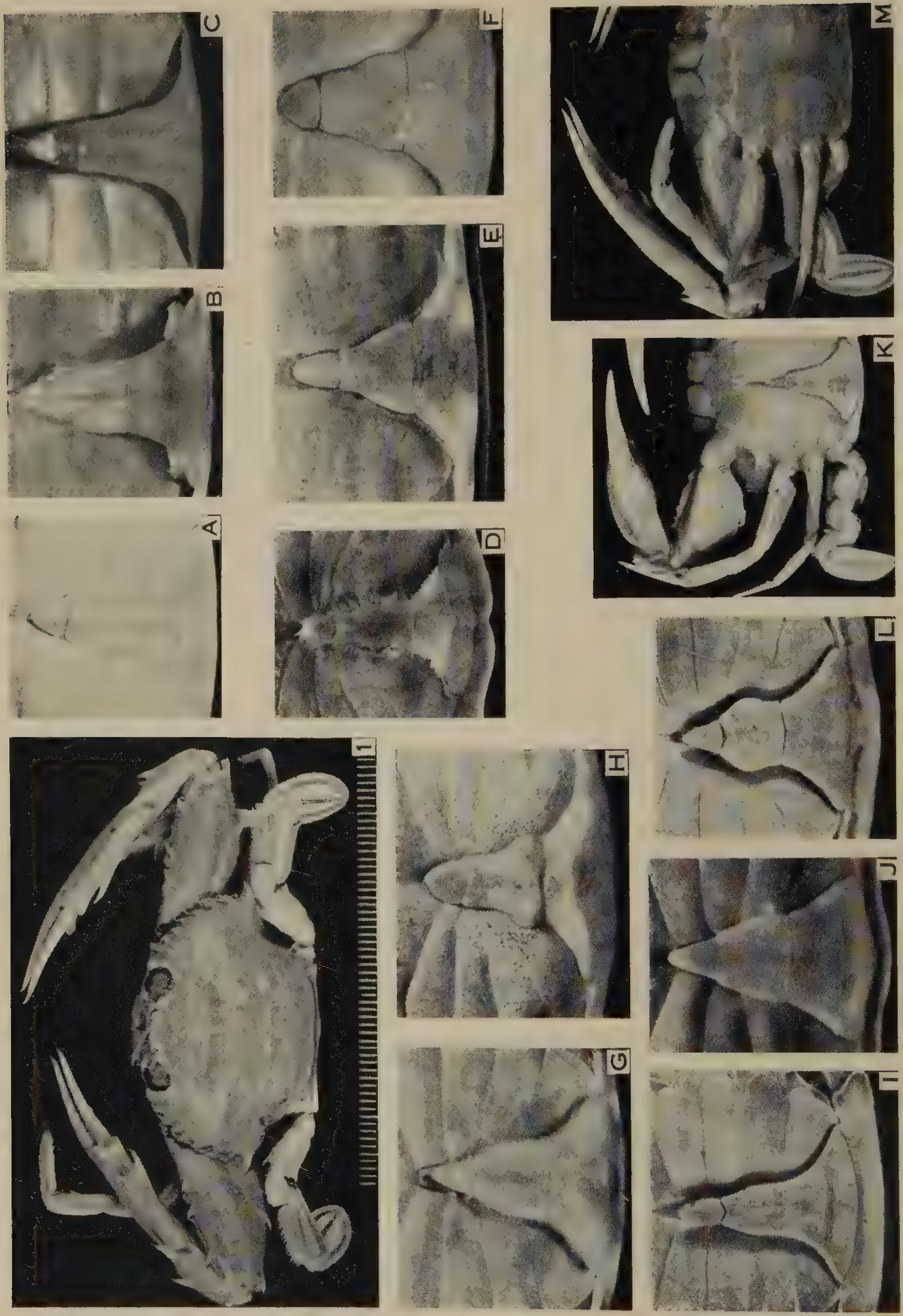
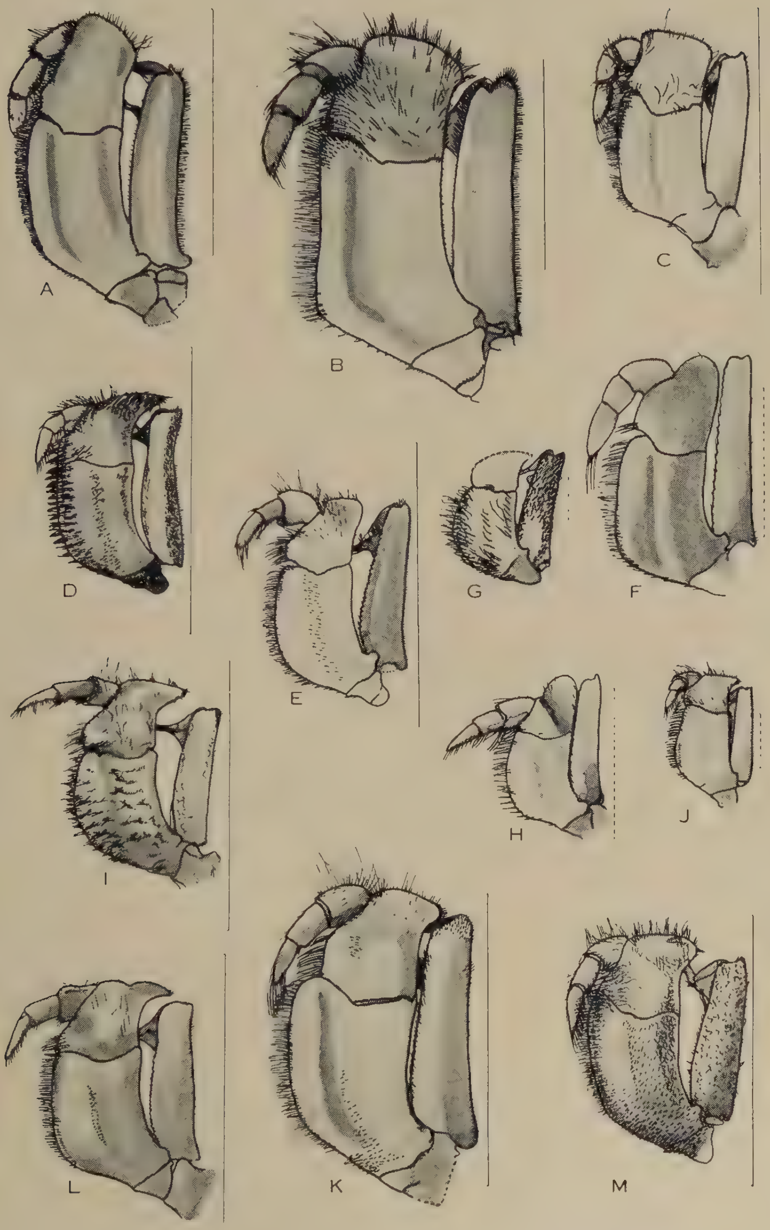


Fig. 1.—Dorsal view of *P. gracilimanus*. Scale divisions, 1 mm. Figs. *A–M*.—Male abdomens of *Portunus* spp. *A*, *P. pelagicus*; *B*, *P. sanguinolentus*; *C*, *P. hastatoides*; *D*, *P. pubescens*; *E*, *P. tenuipes*; *F*, *P. longispinosus*; *G*, *P. brocki*; *H*, *P. emarginatus*; *I*, *P. granulatus*; *J*, *P. gladiator*; *K*, *P. rubromarginatus*; *L*, *P. orbitosinus*; *M*, *P. gracilimanus*.

AUSTRALIAN PORTUNIDS. III



Wash drawings of third maxillipeds. *A*, *P. pelagicus*; *B*, *P. sanguinolentus*; *C*, *P. pubescens*; *D*, *P. hastatoides*; *E*, *P. tenuipes*; *F*, *P. longispinosus*; *G*, *P. brocki*; *H*, *P. emarginatus*; *I*, *P. granulatus*; *J*, *P. gladiator*; *K*, *P. rubromarginatus*; *L*, *P. orbitosinus*; *M*, *P. gracilimanus*. Scale lines: full lines, 1 cm; broken lines, 2 cm.

DETERMINATION OF AGE IN THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough*

[*Manuscript received February* 10, 1959]

Summary

The use of baleen, ear plugs, and ovaries in the determination of age in humpback whales is described.

From the evidence of baleen, the majority of humpback whales reach puberty at 4 or 5 years of age.

The rate of accumulation of laminations in ear plugs is two laminations per year. The mean rate of ovulation in sexually mature females is 1·1 per year. Age determination upon the same sample of mature females by these two methods gives very similar distribution of ages.

The age distribution within separate sexes from samples of mature humpback whales examined on the west and east coasts of Australia in 1957 are compared. The results indicate that the population migrating along the west coast is at present composed of younger individuals than that on the east coast of Australia.

I. Introduction

In a study of whale populations it is necessary to determine the ages of individuals and so obtain the age distribution within samples of these populations.

One of the methods of age determination which showed promise in earlier investigations was the number of ovulations in mature female whales. Mackintosh and Wheeler (1929) pointed out that corpora albicantia appear to persist for a considerable time in the ovaries of whales, the numbers of corpora albicantia being much higher in large physically mature females than in smaller females. It has since been shown (Laws 1958) that corpora albicantia, after some involution, remain in the ovaries of whales as recognizable bodies. Then if the age at puberty and the mean rate of ovulation have been determined for a particular species of whale, the approximate ages of mature females can be calculated.

Various estimates have been made of the rate of ovulation in blue and fin whales (see Nishiwaki 1952; Laws 1958) but this method has not yet been studied intensively in the case of the humpback whale, *Megaptera nodosa* (Bonnaterre). From limited data, Matthews (1937) suggested an average of five ovulations for each 2-year breeding cycle (succeeding the first sexual cycle) in the female humpback whale, but more recent work (Chittleborough 1954) showed this estimate to be too high.

Another useful method of age determination in the Mysticeti was discovered by Ruud (1940) of Norway and independently by Tomilin in Russia (see Ruud 1950). This is based upon periodic growth of the cortical layers in the baleen, as

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shown by seasonal variations in the total thickness of the baleen plate. Age determination from baleen plates has been studied extensively in blue and fin whales (Ruud 1945, 1950, 1955; Ruud, Jonsgård, and Ottestad 1950; Nishiwaki 1952; Hylen, Jonsgård, Pike, and Ruud 1955) but has not yet been applied to humpback whales although seasonal variations in thickness of baleen plates have been demonstrated in this species.

An advantage in using baleen rather than ovaries is that the former method is applicable to both sexes. Unfortunately wear at the free end of baleen plates restricts this technique to the younger individuals.

The recent discovery by Purves (1955) of laminations within the core of ear plugs affords a very promising method of age determination in the Mysticeti, applicable to both sexes and individuals of all ages. This method has been applied to small samples of fin whales (Laws and Purves 1956; Nishiwaki 1957) and humpback whales (Symons and Weston 1958). Assuming two laminations to be laid down in the ear plugs each year, fair agreement was found in ages estimated from ear plugs and from baleen.

In this paper ovulation counts, baleen traces, and ear plug laminations are used for the determination of age in humpback whales. The relationships between these methods are investigated. Mortality curves obtained from samples of two populations of the humpback whale are compared.

II. Material

Baleen traces were obtained from 629 humpback whales (238 males, 391 females) and ear plugs from 657 individuals (370 males, 287 females). In each case the gonads were collected and examined. Some additional baleen samples and ear plugs were collected but not used owing to damage or because of doubtful interpretation. Baleen or ear plugs collected without corresponding gonad data have also been rejected. The material was collected at shore-based whaling stations on the west and east coasts of Australia.

III. Interpretation of Material

(*a*) *Ovaries*

The examination of ovaries has already been described (Chittleborough 1954). As previously stated (Chittleborough 1955*b*) mature female humpback whales taken in Australian waters may have recently ovulated or may be killed during prooestrus. In order to apply a uniform standard in age determination from ovarian data it is intended to consider only the ovulations which had occurred in seasons prior to that of killing. These previous ovulations may be represented either by corpora albicantia alone or may include the corpus graviditatum of females in very advanced pregnancy (as this body represents an ovulation in the previous winter).

(*b*) *Baleen*

Traces were obtained from strips of baleen passed through a recording apparatus constructed from the description given by Ruud (1940). One of the longest baleen plates from each whale was used and care was taken to ensure that the trace was obtained from the gum to the tip of the plate, following a line parallel to the longitudinal fibres within the plate. The portion of baleen which is embedded in the gum is not shown by this method.

In the interpretation of baleen traces from humpback whales it was found that the majority of the traces could be separated into seven typical patterns which are illustrated in Figure 1, the examples given being copies of actual baleen traces. When considering individuals in each of these groups, ovarian and ear plug data showed that the sixth and seventh group were not each of one age class but contained individuals of widely varying ages. For this reason these two baleen groups have been merged into one age group (6+).

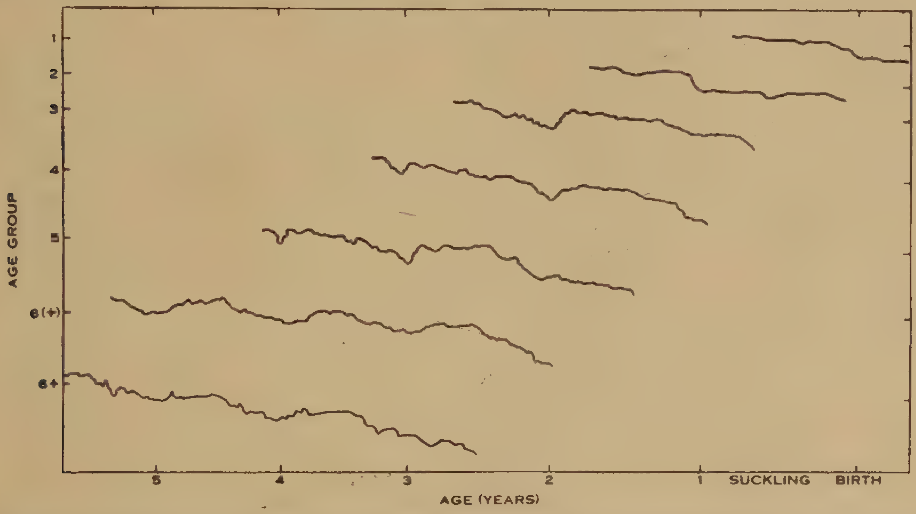

Fig. 1.—Examples of actual traces from baleen plates of humpback whales grouped according to age.

Wear at the tip of baleen plates makes age determination from baleen traces unreliable for individuals more than 6 years of age, so that although a few traces showed four or even five complete growth zones, all whales classified from the baleen as of 6 or more years of age were placed in the 6+ age group.

The example given of a 1-year old individual was taken from a small humpback whale killed under special licence. This female, 28 ft 9 in. long when killed on June 14, was in company with a lactating female and was still suckling, so was estimated to be approximately 10½ months of age.

The remaining age groups illustrated in Figure 1 have been spaced at yearly intervals in accordance with the evidence of Ruud and his co-workers that each growth zone in the baleen represents a span of 1 year.

(c) *Ear Plugs*

Ear plugs were stored in 10 per cent. formalin, then bisected longitudinally with a hand razor after orientating so that the cut surface exposed the widest face of the core of the plug. The face of each surface was then smoothed on a water stone. After cutting, the core of some plugs showed lines of fracture parallel to the laminations. In older (mature) individuals these "fracture lines" were generally regularly spaced, one between each dark band, but in younger (especially immature) whales fracture lines were often irregularly spaced, sometimes in groups, with little relationship to the laminations.

TABLE 1

FEMALE HUMPBACK WHALES: AGE (FROM BALEEN) AND OVARIAN CONDITION

State of Development	Baleen Age Group (Years)											
	1		2		3		4		5		6(+)	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Sexually immature	4	100	8	87·5	22	88·0	23	63·9	33	42·3	14	5·9
At puberty			1	12·5	3	12·0	10	27·8	23	29·5	15	6·3
Sexually mature Ovulations prior to season of killing								8·3		28·2		87·9
1							1		14		38	
2							1		4		73	
3							1		2		45	
4									2		4	
5											4	
6											2	
7											4	
8											2	
9											5	
10											4	
11											4	
12											5	
13											3	
14											2	
15											4	
>15											11	
Total	4		9		25		36		78		239	

In most of the mature individuals the laminations in the core of the ear plug were clearly visible as a succession of dark bands which were narrower and more closely packed towards the base of the ear plug. In the course of this work it was noticed that while the laminations in mature males were almost always regularly spaced and of uniformly decreasing width (see Plate 1), the laminations in mature females frequently (but not always) showed irregularities in width, spacing, or pigmentation (see Plate 2). After a regular series of bands in the upper part of an ear plug, there may be a distinct but narrower, less pigmented lamination, followed by further bands of the earlier type. Sometimes a narrower lamination occurred again after two wider ones. It is suggested that increased nutritional demands in part of the female breeding cycle (pregnancy or lactation) may sometimes coincide with a poorer feeding season, the period of suboptimal nutrition being reflected in the ear plugs. From the available evidence it is suggested that this is more likely to occur in younger mature females (which are still growing) than in older females. Similar irregularities in the laminations were found in both ear plugs from the same individual.

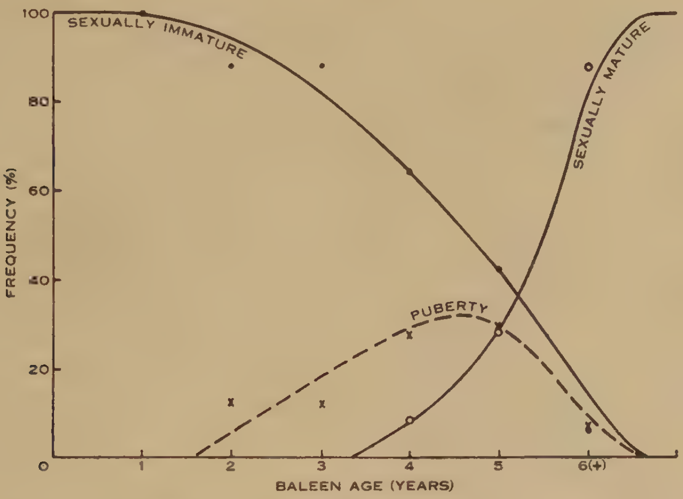

Fig. 2.—Age distribution of sexually immature, puberal, and young mature female humpback whales as determined from baleen plates.

In some ear plugs (less than 10 per cent. of those examined) the laminations were partly or completely obscured by longitudinal striations giving a fibrous appearance to the core of the ear plug (Plate 3). In such cases the ear plugs have been rejected.

The laminations in younger (generally immature) whales were often poorly defined and lacking in pigment (Plate 4, Fig. 1). Sometimes the dark bands could be subdivided into two or three smaller bands placed close together (Plate 4, Fig. 2). In counting the laminations of these ear plugs only the wide, more regularly spaced bands have been used.

Attempts were made to dissect out the ear plugs from near-term foetuses, but only the secretory membranes were found.

IV. Puberty

(a) *Age at Puberty*

Since baleen traces obtained from samples collected on the west and east coasts of Australia gave similar ages at puberty, the data from the two areas are considered together in this regard.

Table 1 shows the ages (as determined from baleen) and ovarian condition of 391 female humpback whales. The proportions of sexually immature, puberal, and sexually mature females in each age group are plotted in Figure 2. The majority of females reach puberty at 4 or 5 years of age, while the upper limit of the age at puberty is close to 7 years.

TABLE 2

MALE HUMPBACK WHALES: AGE (FROM BALEEN) AND MATURITY, CLASSING MALES WITH TOTAL TESTES WEIGHT EXCEEDING 4 KG AS SEXUALLY MATURE

Baleen Age Group (Years)	Total No.	Sexually Immature		Sexually Mature	
		No.	(%)	No.	(%)
1	1	1	100		
2	14	14	100		
3	25	21	84·0	4	16·0
4	35	24	68·6	11	31·4
5	62	24	38·7	38	61·3
6(+)	101	10	9·9	91	90·1

Table 2 and Figure 3 show the ages (from baleen) and sexual condition in 238 male humpback whales, classing males with total testes weight exceeding 4 kg as sexually mature (Chittleborough 1955*a*). In males the mean age at puberty lies between 4 and 5 years; it is probable that slightly more males reach puberty at 5 years than at 4 years of age.

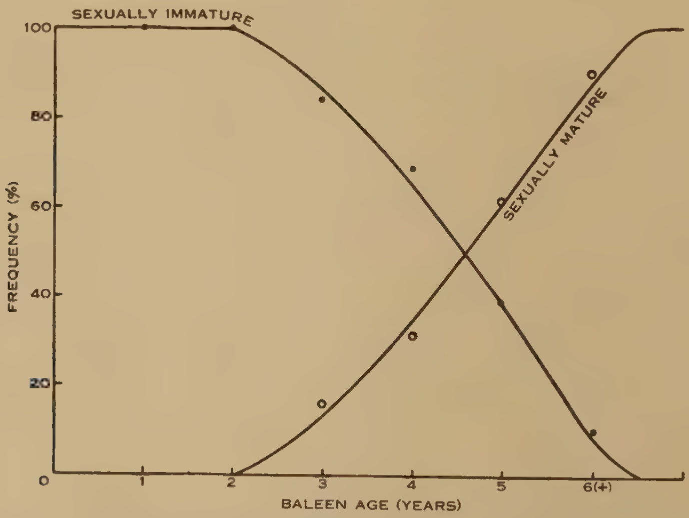

Fig. 3.—Age distribution of sexually immature and young mature male humpback whales as determined from baleen plates.

(*b*) *Ear Plugs at Puberty*

Table 3 shows the distribution of the numbers of ear plug laminations from 290 female humpback whales classified according to ovarian condition. This shows that at puberty the ear plugs may contain from five to 14 laminations with a mean of close to nine laminations.

Figure 4 shows the distribution of the numbers of ear plug laminations from 166 humpback whales grouped according to age (from baleen). In each year class the modal number of ear plug laminations lies at (or very close to) twice the number of years of age. Since most humpback whales reach puberty at 4 and 5 years of age, the mean number of laminations in the ear plugs at puberty is between eight and ten laminations.

TABLE 3

DISTRIBUTION OF NUMBERS OF EAR PLUG LAMINATIONS FROM 290 FEMALE HUMPBACK WHALES CLASSIFIED ACCORDING TO OVARIAN CONDITION

Number of Ear Plug Laminations	Numbers of Females		
	Sexually Immature	Puberal	Sexually Mature
4	1	—	—
5	3	2	—
6	6	3	—
7	7	2	2
8	6	—	5
9	2	4	4
10	4	2	11
11	1	2	12
12	—	1	16
13	—	—	17
14	1	—	17
15	—	—	7
16	—	—	14
>16	—	—	138

Much of the variation in the numbers of ear plug laminations within any one year class shown in Figure 4 may be attributed to poorly defined laminations often found in ear plugs of young whales (see Section III(*c*)).

V. RATE OF OVULATION IN MATURE FEMALES

The only direct method for determining the rate of ovulation in female whales is to mark calves or yearlings and examine the ovaries of the females when marked individuals are killed in later years. Little information of this type is available to date. One female humpback whale marked on the west coast of Australia when it was accompanied by a calf was killed and examined 9 years later. The ovaries then contained ten corpora albicantia, so that if this female had been marked at the end of its first pregnancy, the average rate of ovulation would have been 1·0 ovulation per year.

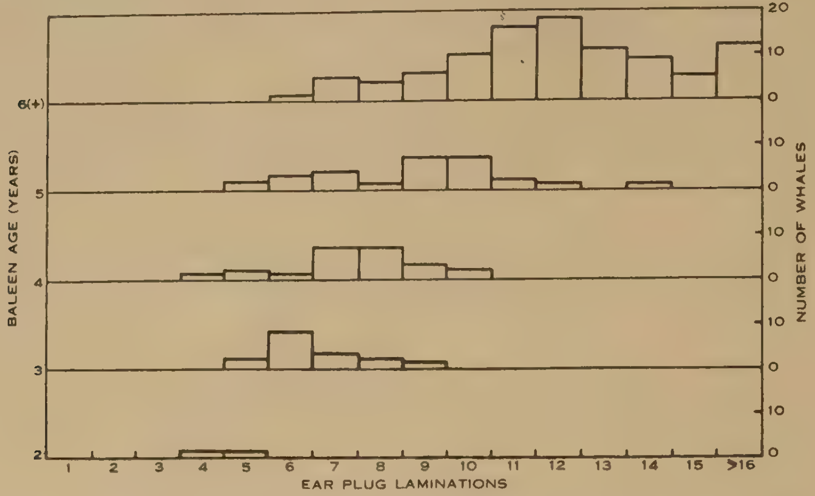

Fig. 4.—Relationship between age as determined from baleen plates and numbers of ear plug laminations in young humpback whales.

More precise information is available from another female which was also marked and later killed on the west coast of Australia. This female was accompanied by a small calf when marked in August 1954, so must have ovulated at least once in the winter of 1953. When killed in September 1956, the ovaries contained three corpora albicantia and one newly formed corpus luteum, while the ear plugs contained 14 laminations. Table 4 shows four variations in the possible sequence of ovulations in this female. It is probable that one of the first three variations actually occurred, in which case this female matured at 4 years of age (becoming pregnant) and had an average of one ovulation per year up to the time of killing.

Table 4

INFORMATION COLLECTED AND INFERRED FROM MARK A99, FIRED INTO A FEMALE WITH SMALL CALF ON AUGUST 17, 1954, RECOVERED ON SEPTEMBER 22, 1956

Possible Sequences of Ovulations	1952	1953	1954	1955	1956
Variation (*a*)	immature	2 ovulations	—	1 ovulation	1 ovulation
Variation (*b*)	immature	1 ovulation	—	2 ovulations	1 ovulation
Variation (*c*)	immature	1 ovulation	1 ovulation (post-partum)	1 ovulation	1 ovulation
Variation (*d*)	1 ovulation	1 ovulation	—	1 ovulation	1 ovulation
Number of ear plug laminations	6	8	10	12	14

TABLE 5

OVULATIONS OCCURRING IN 100 SEXUALLY MATURE FEMALE HUMPBACK WHALES DURING A 2-YEAR BREEDING CYCLE

(*A*) First Winter			(*B*) Second Winter		
Number of Females	Sexual Condition	Number of Ovulations	Number of Females	Sexual Condition	Number of Ovulations
5	No oestrous cycles	0	5	Oestrous cycles at same rate as in *A* (1·2 per female)	6
73	One oestrous cycle	73	5	Fail to conceive at *A* or lose early embryo so experience oestrous cycles as in *A*	6
19	Two oestrous cycles	38	5	Become pregnant in *A* but lose calf at birth so experience oestrous cycles as in *A*	6
3	Three oestrous cycles	9	10	Successfully give birth to calf conceived in *A*, then experience a post-partum ovulation (becoming pregnant while lactating)	10
			75	Successfully give birth to calf conceived in *A*, then may experience a post-partum ovulation, but this does not result in conception	0–75
100		120			28–103

In female humpback whales breeding cycles are of 2 years' duration and so extend over two winter periods when ovulation normally occurs (Chittleborough 1958*a*, Fig. 4). It is proposed here to estimate the total number of ovulations which occur in 100 females in the course of 2 years, considering the possible variations within the breeding cycle.

Ovulations occurring in sexually mature, non-pregnant females entering the first ovulatory period of a breeding cycle have already been studied (Chittleborough 1954). From this and further material it is estimated that in this period 100 mature females ovulate as given in part (*A*) of Table 5. The average number of ovulations per female in the first winter of a breeding cycle is then 1·2 ovulations.

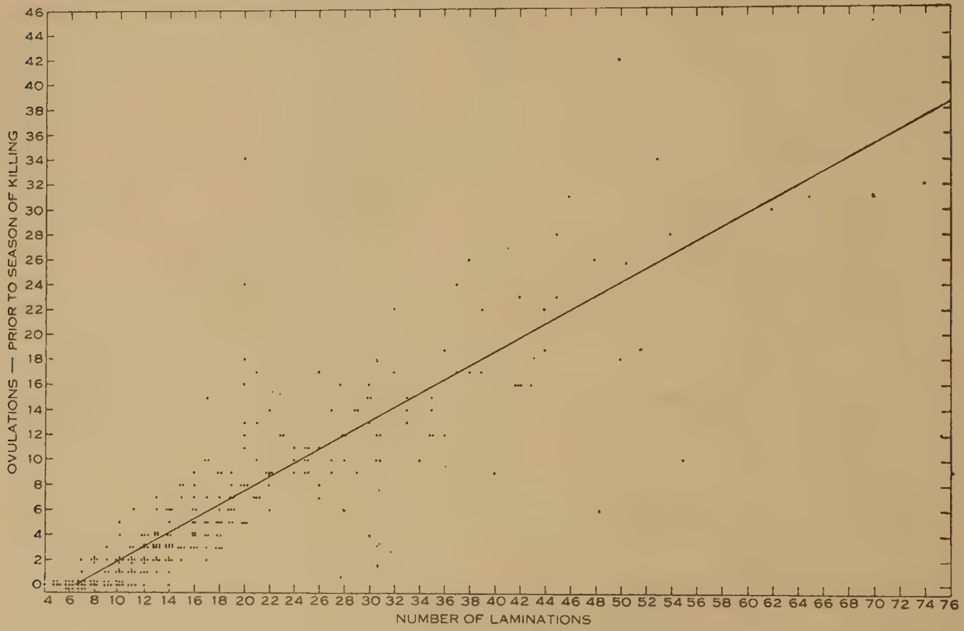

Fig. 5.—Relationship between numbers of previous ovulations and numbers of laminations in the ear plugs, for 287 female humpback whales.

Full details of ovarian activity in the second winter of the breeding cycle are difficult to obtain owing to the regulation prohibiting the killing of females accompanied by calves. The various conditions shown in part (*B*) of Table 5 have been found and described (Chittleborough 1958*a*), but the relative proportions given for each are largely speculative. Although post-partum ovulation does occur in the humpback whale (sometimes resulting in a female being simultaneously pregnant and lactating), it is not possible to determine by direct observation how often this occurs.

From the data given in Table 5, if post-partum ovulation is of infrequent occurrence, the total number of ovulations from 100 mature females in a 2-year breeding cycle is 148, while if post-partum ovulation is of regular occurrence the total number of ovulations is 223. Then the average rate of ovulation for mature female humpback whales lies between 0·74 and 1·12 ovulations per year.

VI. RELATION BETWEEN OVARIAN AND EAR PLUG DATA FROM FEMALES

In Figure 5 the number of ear plug laminations is plotted against the number of previous ovulations for each of 287 female humpback whales. The regression line calculated by the method of least squares is also shown. A few of the points lie very considerably above or below the regression line. This might be the result of unusually fast or slow rates of ovulation which may sometimes occur in individual

TABLE 6

DISTRIBUTION OF OVULATION COUNTS AND NUMBERS OF EAR PLUG LAMINATIONS, WITH CORRESPONDING SURVIVAL VALUES, FROM 158 SEXUALLY MATURE FEMALES

Ovaries				Ear Plugs			
Number of Previous Ovulations	Number of Females	Survivors		Number of Laminations	Number of Females	Survivors	
		No.	(%)			No.	(%)
		158	100			158	100
1	13	145	91·8	<10	18	140	88·6
2	28	117	74·1	12	23	117	74·1
3	16	101	63·9	14	23	94	59·5
4	15	86	54·4	16	13	81	51·3
5	8	78	49·4	18	14	67	42·4
6	9	69	43·7	20	15	52	32·9
7	8	61	38·6	22	8	44	27·8
8	7	54	34·2	24	5	39	24·7
9	10	44	27·8	26	8	31	19·6
10	8	36	22·8	28	6	25	15·8
11	2	34	21·5	30	6	19	12·0
12	6	28	17·7	32	3	16	10·1
13	4	24	15·2	34	2	14	8·9
14	4	20	12·7	36	1	13	8·2
15	3	17	10·8	38	1	12	7·6
16	5	12	7·6	40	1	11	7·0
17	4	8	5·1	42	3	8	5·1
18		8	5·1	44	3	5	3·2
19	1	7	4·4	46		5	3·2
20		7	4·4	48	1	4	2·5
21		7	4·4	50	1	3	1·9
22	2	5	3·2	52		3	1·9
23		5	3·2	54		3	1·9
24	1	4	2·5	56	2	1	0·6
25		4	2·5	58		1	0·6
26		4	2·5	>58	1		
27		4	2·5				
28		4	2·5				
29		4	2·5				
30	1	3	1·9				
>30	3						

females. It is also possible that one or two of the points well above the regression line might represent females whose ear plugs were of fibrous appearance (though not as fibrous as shown in Plate 3), so that laminations were partially obscured; this would result in much lower counts of laminations than were actually present.

The slope of the regression line ($y = 0{\cdot}558x - 3{\cdot}635$) gives the relationship of two ear plug laminations as equal to 1·12 ovulations. From this relationship it is possible to compare the mortality curves obtained from the same sample of mature females using the laminations in ear plugs and numbers of previous ovulations as independent methods of age determination. Table 6 shows the distribution of ovulation counts and numbers of ear plug laminations, with corresponding survival values, from 158 sexually mature female humpback whales sampled at random from the catch made at Carnarvon in 1957. The mortality curves derived from the two sets of data are shown in Figure 6, the scales on the abscissa axis being in the ratio of 2 ear plug laminations to 1·1 ovulations. The two curves are almost identical, showing good agreement between the two methods as applied.

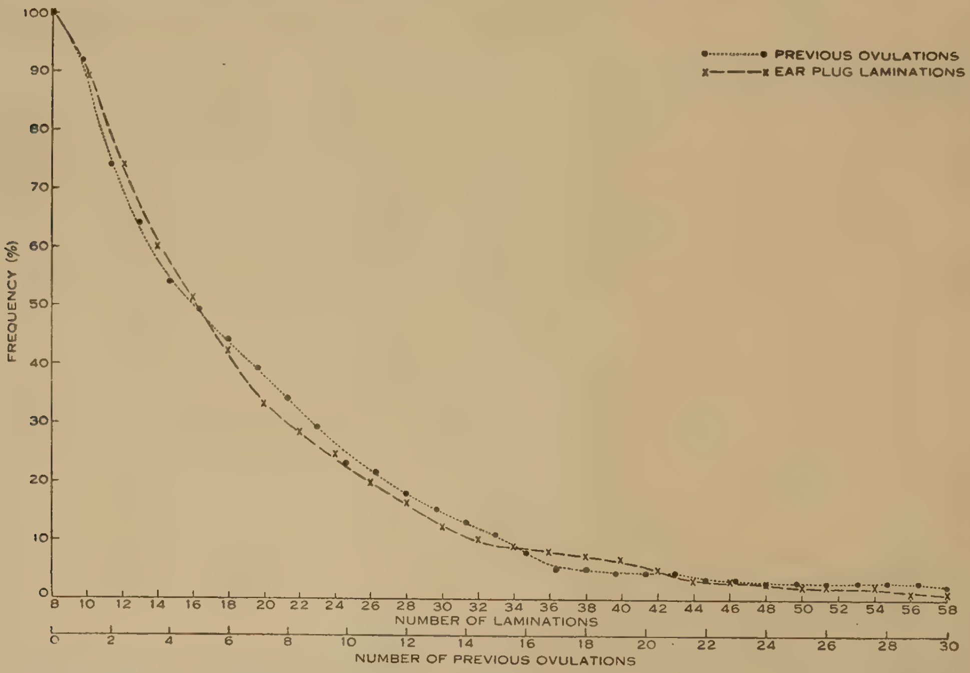

Fig. 6.—Mortality curves derived from the numbers of previous ovulations and from the numbers of ear plug laminations, for the same sample of 158 sexually mature female humpback whales.

VII. Comparison of Samples from Two Populations of Humpback Whales

Shore-based whaling stations on the west and east coasts of Australia operate upon separate populations of humpback whales known as Group IV and Group V respectively (see Mackintosh 1942). Using the methods described above it is possible to compare the age distribution within samples taken from these two populations.

TABLE 7

DISTRIBUTION OF NUMBERS OF EAR PLUG LAMINATIONS FROM SAMPLES OF TWO POPULATIONS

Number of Ear Plug Laminations	Mature Females				Mature Males			
	Carnarvon (Group IV)		Moreton Island (Group V)		Carnarvon (Group IV)		Moreton Island (Group V)	
	No. of Whales	(%)	No. of Whales	(%)	No. of Whales	(%)	No. of Whales	(%)
<10	18	11·4	2	2·7	53	33·1	13	7·9
12	23	14·6	3	4·1	22	13·8	17	10·3
14	23	14·6	9	12·3	22	13·8	9	5·5
16	13	8·2	7	9·6	14	8·8	12	7·3
18	14	8·9	8	11·0	11	6·9	9	5·5
20	15	9·5	6	8·2	7	4·4	11	6·7
22	8	5·1	4	5·5	6	3·8	11	6·7
24	5	3·2	1	1·4	1	0·6	8	4·8
26	8	5·1	3	4·1	4	2·5	10	6·1
28	6	3·8	2	2·7	4	2·5	6	3·6
30	6	3·8	2	2·7	2	1·3	8	4·8
32	3	1·9	3	4·1	2	1·3	6	3·6
34	2	1·3	2	2·7	1	0·6	4	2·4
36	1	0·6	4	5·5			6	3·6
38	1	0·6	3	4·1	1	0·6	2	1·2
40	1	0·6	1	1·4	2	1·3	3	1·8
42	3	1·9	2	2·7			2	1·2
44	3	1·9			1	0·6	4	2·4
46			3	4·1			3	1·8
48	1	0·6	1	1·4				
50	1	0·6	1	1·4	2	1·3	2	1·2
52					2	1·3	2	1·2
54			1	1·4			2	1·2
56	2	1·3					5	3·0
58								
60							2	1·2
62	1	0·6					1	0·6
64							1	0·6
66			1	1·4			1	0·6
70			2	2·7				
72							1	0·6
74			1	1·4			1	0·6
76			1	1·4	1	0·6	1	0·6
80					1	0·6		
84					1	0·6		
86							1	0·6
96							1	0·6
Total	158		73		160		165	

It is proposed here to consider only the sexually mature individuals. By doing so possible differences in gunner selection between the two areas would be minimized. Also by considering only mature whales the results are comparable with mortality curves calculated for samples of other species from Antarctic waters, using only pregnant females (see the reports to the International Whaling Commission for 1955 and 1958).

The samples compared were taken from Carnarvon (west coast) and Moreton Island (east coast) in 1957.

Table 7 shows the distribution of the numbers of ear plug laminations from the two samples. Figure 7 shows the percentage frequency distribution of the ear plug laminations for the females from the two samples, showing also the length frequency distribution and mean lengths of the same females. Although there is little difference between either the mean lengths or the length frequency distribution in the two samples, the distribution of ages (from the ear plugs) is quite different, there being more young females and less of the older individuals in the sample of females from the west coast than in that from the east coast of Australia.

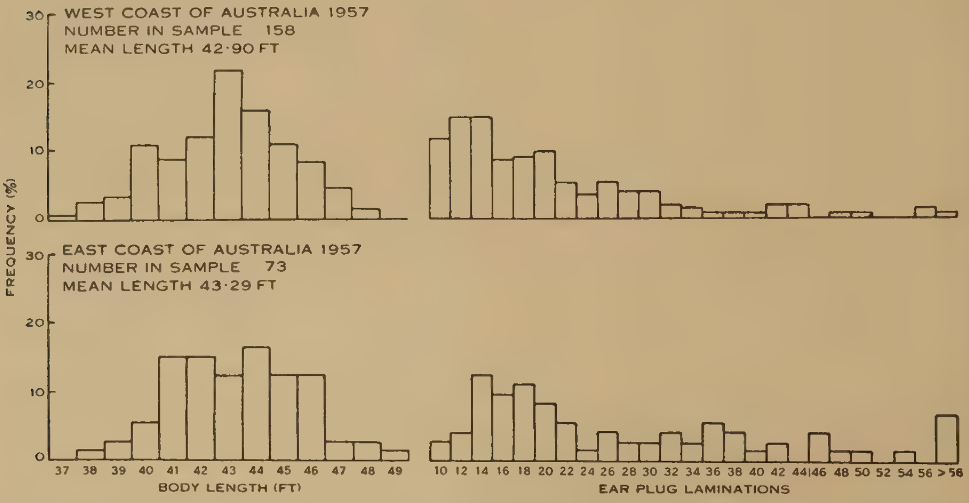

Fig. 7.—Mean lengths, length frequency distributions, and distribution of ages (from ear plug laminations) for samples of sexually mature females from the west and east coasts of Australia in 1957.

Figure 8 shows the corresponding information for the males sampled in the two areas. In this case there is some difference in the mean lengths, considerable difference in the length frequency distribution, and a great difference in the distribution of ages (from the ear plugs), the sample from the west coast containing far more young mature males.

Figure 9 shows mortality curves constructed from the data in Table 7. The variations in the curve representing the females sampled on the east coast of Australia are probably the result of the smaller sample, but the curve generally follows that of the males sampled in the same locality. The mortality curve derived for the mature males examined on the west coast is steeper than that of the corresponding sample of females, and both are much steeper than the mortality curves of either males or females from the east coast of Australia.

VIII. Discussion

Seasonal variations in the thickness of the cortical layers of the baleen afford a useful method of age determination in both sexes for the first 5 years of life (up to puberty) but wear at the tip of baleen plates prevents their use for determining the age of older (mature) individuals. Baleen traces from the younger individuals have proved most useful in establishing the rate of accumulation of laminations within the core of ear plugs.

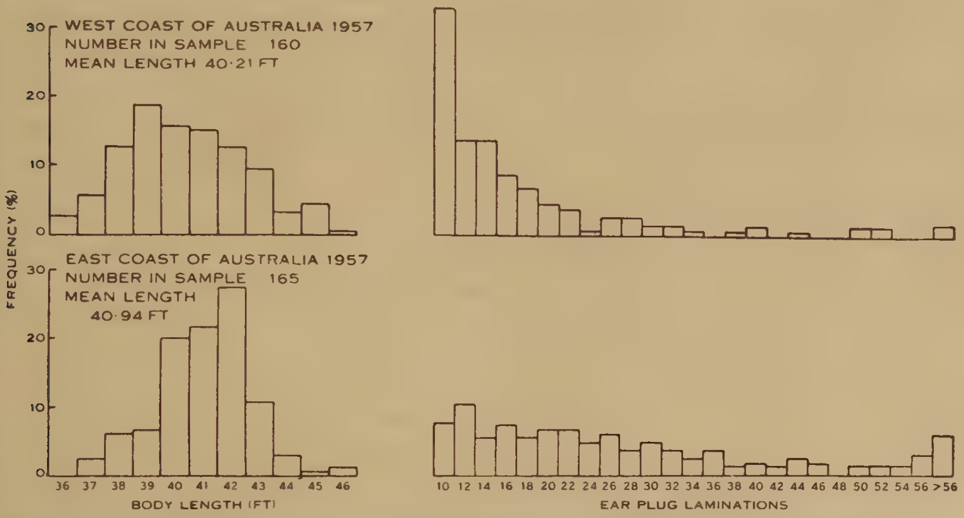

Fig. 8.—Mean lengths, length frequency distributions, and distribution of ages (from ear plug laminations) for samples of sexually mature males from the west and east coasts of Australia in 1957.

From the examination of the auditory meatus of near-term foetuses it would appear that the first lamination of the ear plug is laid down soon after birth. Thereafter two laminations are formed each year. At puberty a mean of nine laminations are present.

It has been pointed out that the laminations within the ear plugs of young (immature) whales are often poorly defined and lacking in pigment. As these earlier laminations become compressed at the top of the ear plug core during later years of life they may become more difficult to distinguish so that counts of the laminations in the ear plugs of mature individuals may be slightly below the actual number laid down. For this reason the ages of mature whales as determined from the ear plugs should be regarded as minimum ages. However, assuming the possible error to be slight and relatively constant, the ear plugs afford the best method available at present for age determination in the Mysticeti.

The regression line representing the relationship between numbers of ear plug laminations and numbers of previous ovulations (Fig. 5) passes through the abscissa axis at 6·5 ear plug laminations instead of between 8 and 10 laminations as shown by other methods. This is the result of the tendency for the counts of laminations within the ear plugs of mature individuals to be slightly below the actual number present. Most of the data used in the calculation of this regression line were obtained from mature females.

Since the possible error in counts of ear plug laminations is considered to be fairly constant in the mature females, the slope of this regression line is close to the true relationship, so that after attainment of puberty two ear plug laminations are equivalent to an average of 1·1 ovulations. This is circumstantial evidence in support of the theory that post-partum ovulation is of common occurrence (although perhaps not often successful) in the female humpback whale, as it has been shown from the examination of ovaries (Section V) that if post-partum ovulation is of regular occurrence the mean rate of ovulation would be 1·12 ovulations per year.

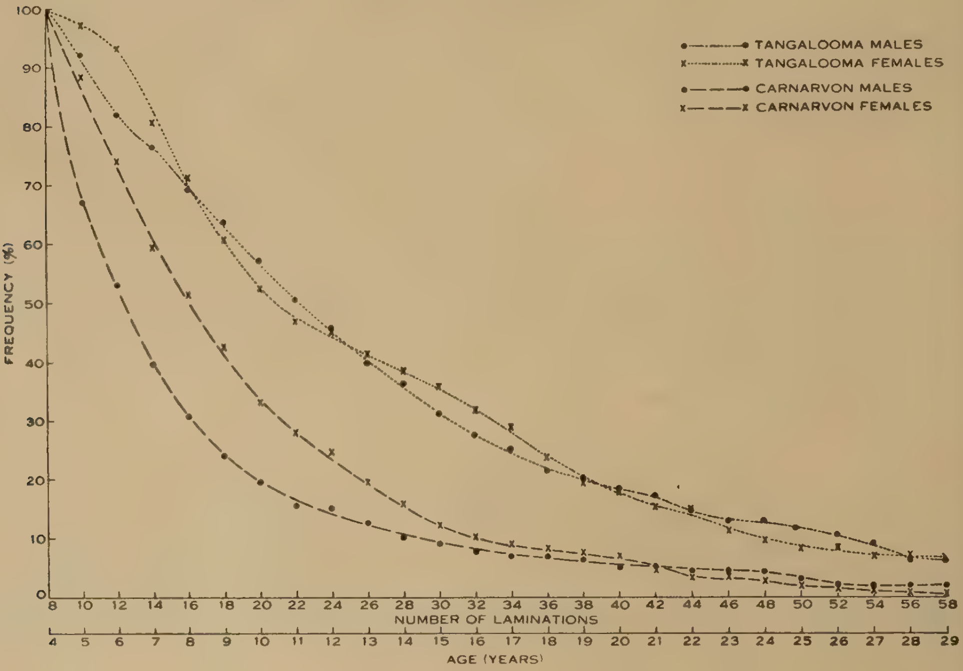

Fig. 9.—Mortality curves for mature male and female humpback whales sampled in 1957 on the east coast at Tangalooma and on the west coast at Carnarvon.

The regression line representing the relationship between numbers of ear plug laminations and numbers of previous ovulations ($y = 0 \cdot 558x - 3 \cdot 635$) is similar to that obtained by Symons and Weston (1958) for approximately 30 female humpback whales taken in Antarctic waters ($y = 0 \cdot 59x - 3 \cdot 4$). In this case two ear plug laminations would be equivalent to 1·18 ovulations.

Since the mortality curves derived separately for the same females using ear plug laminations and numbers of previous ovulations are the same when plotted on the scale ear plug laminations : previous ovulations = 2 : 1·1, the two methods may replace each other in samples of mature females where complete data were obtained from only one of these organs.

When determining the age of a single whale by the three methods studied in this paper, the method using baleen plates is considered to be the most accurate for a whale of up to 5 years of age, while for an older female the number of laminations within the ear plugs gives a much more reliable index of age than the number of previous ovulations. Figure 5 shows that if the rate of accumulation of ear plug laminations is constant throughout life, then the rate of ovulation may vary considerably from one female to another. The rate of ovulation may also vary between puberty and old age within each individual. For these reasons the age of a mature female as estimated from the number of previous ovulations (using an average of 1·1 ovulations per year, and a mean age of 4 or 5 years at puberty) gives only a "mean age" of that female. Although this may be less accurate than the age as determined from ear plug laminations, the method using numbers of previous ovulations gives a useful index of the age distribution within a large sample of mature females.

In the comparison of age distribution and mortality curves obtained from collections of ear plugs from sexually mature individuals from the west and east coasts of Australia in 1957, it has been shown that the sample from the west coast contained a far higher proportion of young individuals than present in the sample collected on the east coast.

This difference cannot be attributed to differences in the times of passage of various age groups past the sampling points in the two localities, as the samples were collected in similar latitudes and throughout the northward migration of the humpback whales on the west and east coast of Australia.

Assuming that the samples were representative of the mature individuals in the populations passing along these coasts in that year, the evidence from age distribution and mortality curves strengthens the previous evidence (Chittleborough 1958*b*) of a decline in the Group IV stock of humpback whales. Further, the steeper mortality curve for males than for females sampled on the west coast indicates that the mature males in that stock have been affected more than the mature females. The explanation of this is based on the fact that males reach puberty at considerably shorter lengths than females. In earlier years (from 1949) the intense catching from the Group IV stock has been concentrated upon mature individuals in the case of the males, but spread over a wider range of age groups, including more immature individuals, in the case of the females. As a result of this, by 1957 fewer older males than females remained in this population.

When comparing the age distribution in the samples from the two stocks it might be argued that more careful selection on the east coast resulted in more of the older individuals being taken in this area than in the catch made on the west coast. As stressed earlier, in the comparison of samples from the two areas (Section VII) only mature individuals have been used. This minimizes possible differences in the degree of selection because after sexual maturity has been attained the rate of growth is less and decreases fairly rapidly in succeeding years.

Although it is not possible to measure and compare the "selection factor" as applied by individual gunners or by gunners in different localities, it is considered that the evidence based upon age distribution as determined from ear plugs shows that at present there are real differences in the age distribution of the two populations of humpback whales which migrate along the west and east coasts of Australia respectively.

It is well known from population studies upon other animals that commercial operations (or other sampling by man) upon an accumulated population initially cause a reduction in the proportion of old individuals in that population, which may then stabilize at a lower mean age (Nicholson 1954). However, from the comparison of the age distribution (over several years) in samples of humpback whales from the west and east coasts of Australia it would appear that the population migrating along the west coast has not stabilized during several years of commercial catching, but is continuing to decline.

IX. Acknowledgments

The cooperation of the Norwest Whaling Company, Cheynes Beach Whaling Company, and Whale Products Pty. Ltd., enabling material to be collected from their respective stations at Carnarvon, Albany, and Moreton Island is acknowledged.

Commonwealth and State Fisheries Inspectors gave valuable assistance in the collection and sorting of material.

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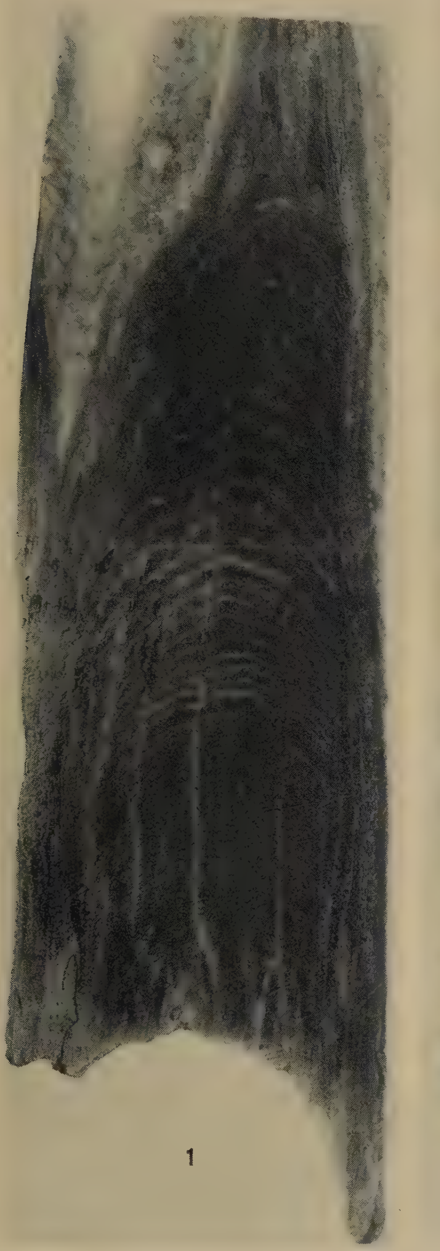
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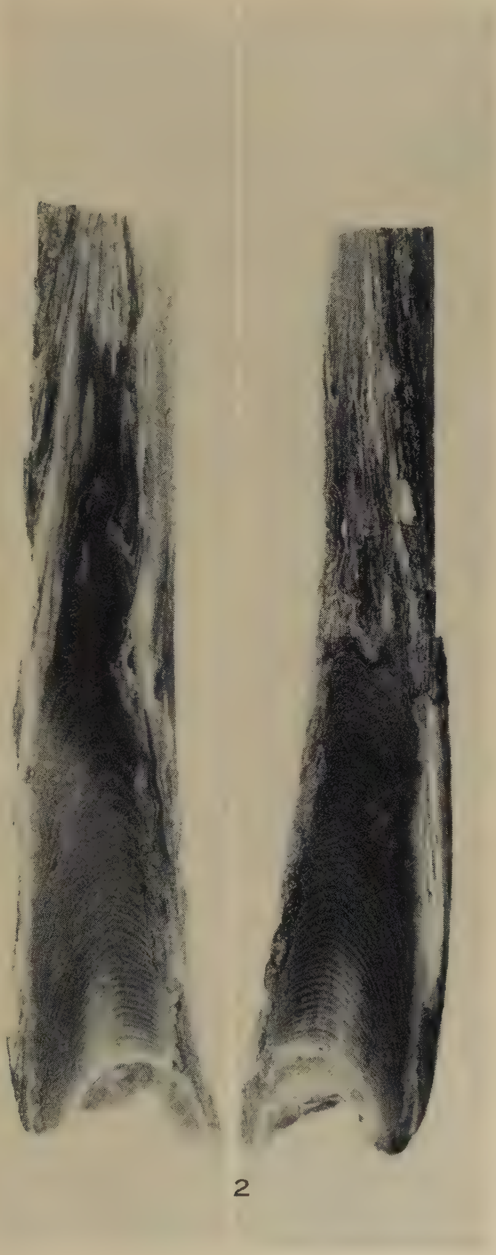
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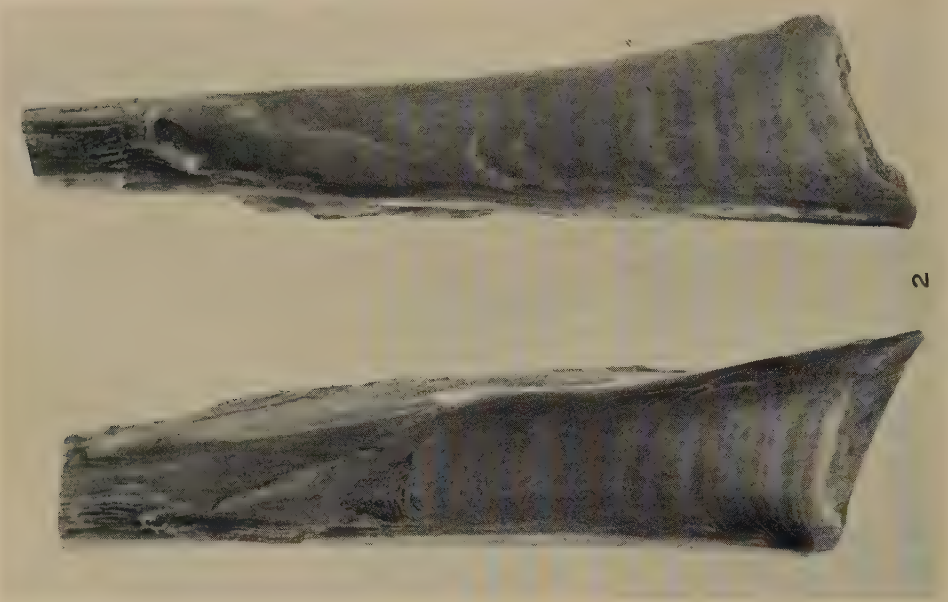
Fig. 1.—Ear plug from a mature male humpback whale: 95 regular laminations (very crowded at the base).

Fig. 2.—Ear plugs from a mature male humpback whale: 36 regular laminations.

DETERMINATION OF AGE IN HUMPBACK WHALES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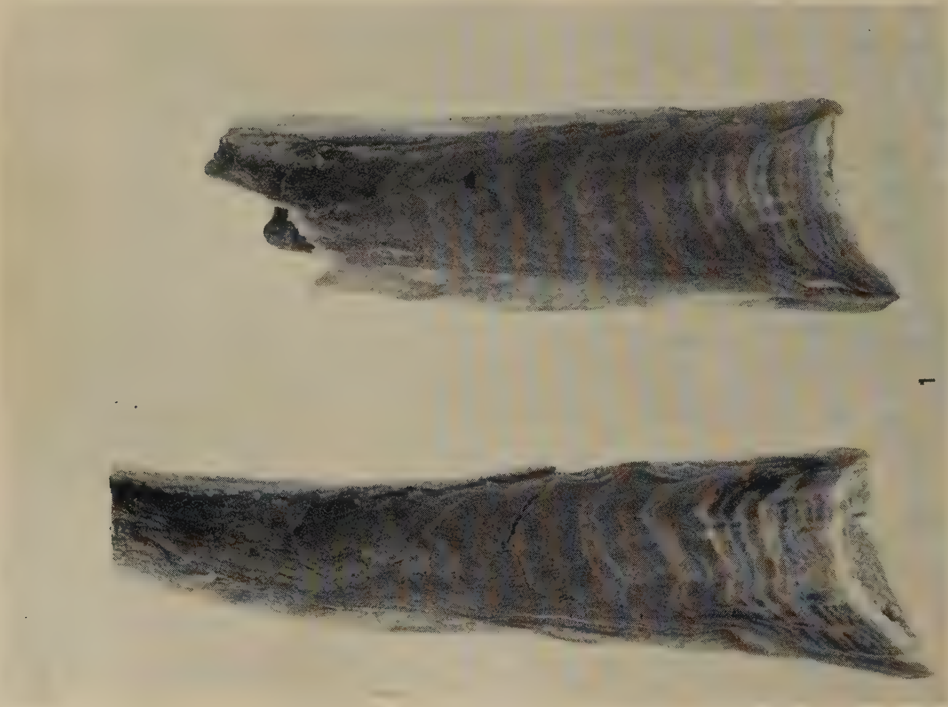
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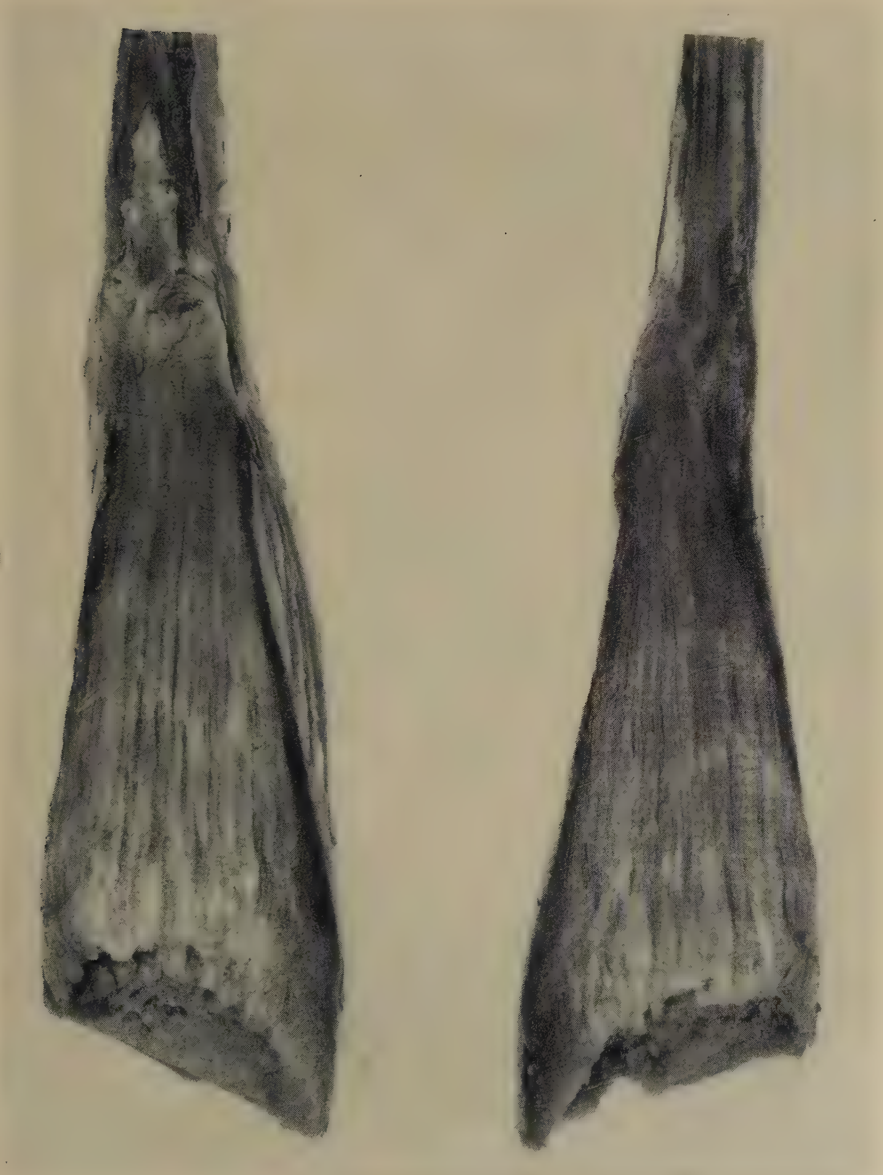
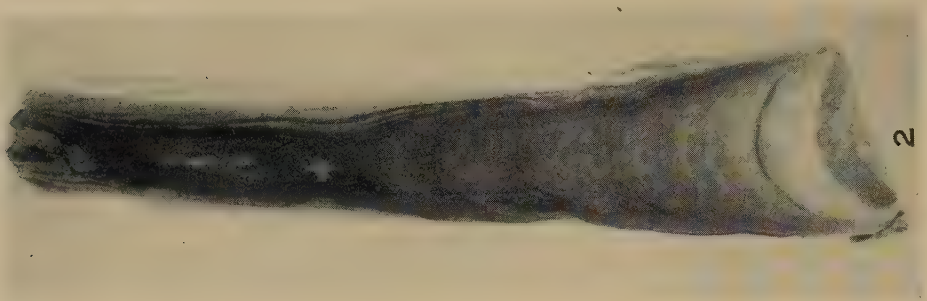
Fig. 1.—Left and right ear plugs from a mature female: 22 laminations, some irregularities in width and pigmentation. Eight corpora albicantia recorded from the ovaries.

Fig. 2.—Left and right ear plugs from a mature female: 22 laminations, lower ones irregular in width. Six corpora albicantia recorded from the ovaries.



Ear plugs of fibrous appearance, rejected as no reliable count of laminations was possible.

DETERMINATION OF AGE IN HUMPBACK WHALES



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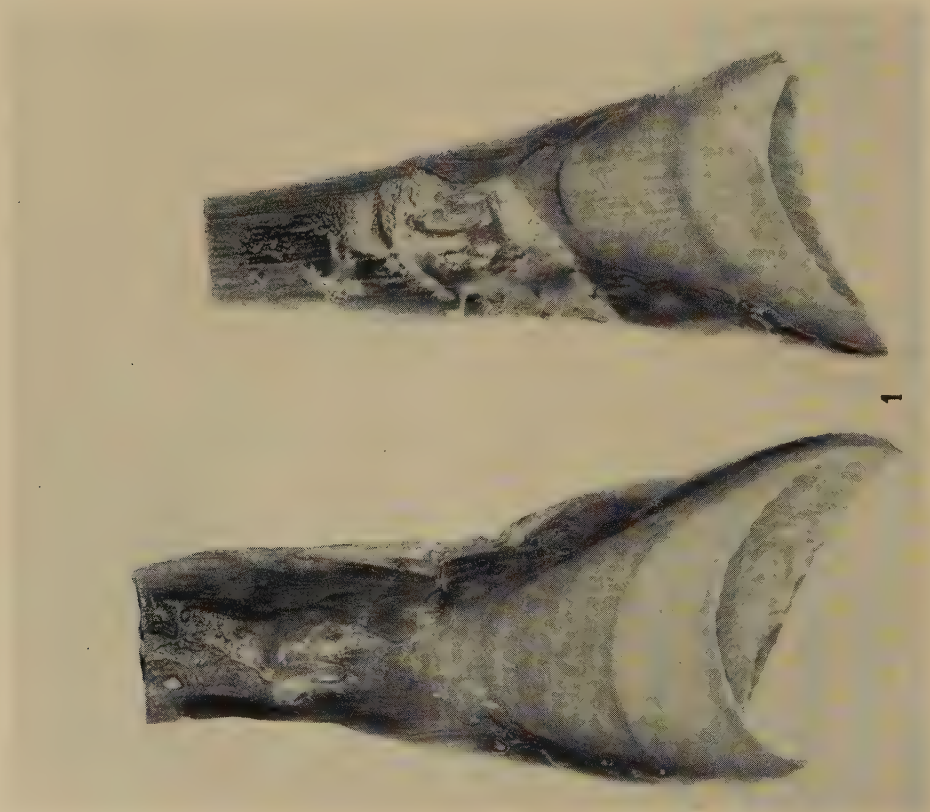

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Fig. 1.—Ear plugs from an immature male (length 33 ft 5 in.). Approximately five pale, poorly defined laminations.

Fig. 2.—Ear plug from a young (recently matured) male: 11 laminations, most broken by lines of fracture.

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THE NATURALIZATION OF THE PACIFIC OYSTER IN AUSTRALIA

By J. M. Thomson*

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Summary

The pacific oyster, *Crassostrea gigas* Thunberg, has been successfully transplanted from Japan to southern Australia. Mortality was heavy amongst those transported by ship (20 days out of water), but negligible amongst those brought in by air (4 days out of water). The rate of growth has been greater than that of native oysters. Although the spatfall has been slight and irregular at other test sites, successful spatfalls have occurred in Port Sorell for three successive seasons. From Port Sorell natural spread has taken place to the Mersey River to the west and to the Tamar River to the east.

I. Introduction

A previous paper (Thomson 1952) described the first successful importations of the Pacific oyster, *Crassostrea gigas*, to Tasmania in southern Australia and the rate of growth attained by the species in its new environment. Other oysters set out at the same time in Western Australia failed to survive the first winter. This paper describes the further field experiments carried on since 1951.

II. Importation of Stocks

Thomson (1952) previously expressed the opinion that a high rate of survival of Pacific oysters during shipment could be achieved by reducing the travelling time between Japan and Australia to 14 days or less. This had been achieved by shipping prior to 1941; but when in 1951 it was decided to augment the stocks already accumulated in Tasmania it was found that direct movement of ships from Japan had not been resumed, there being intermediate stops which prolonged the voyages. Therefore it was decided to attempt an importation by air.

A trial shipment of five cases was flown to Australia in November 1951. As this succeeded without any appreciable mortality a further 75 cases were brought by air in September 1952. Again no mortality occurred. These later importations were all set out in Pittwater, Tasmania, where the earlier stocks had been acclimatized, for 12 months quarantine against the importation of pests. The sequence of importations is summarized in Table 1 (p. 146).

III. New Oyster Beds

In May 1952, as very little spat from known spawnings had been detected in Pittwater, a few test trays were transferred to Port Sorell on the north coast of Tasmania (Fig. 1). Port Sorell was chosen both because its physiography seemed

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suitable and because summer temperatures, which could be a decisive factor in successful breeding, remained high for longer periods than in Pittwater (Fig. 2).

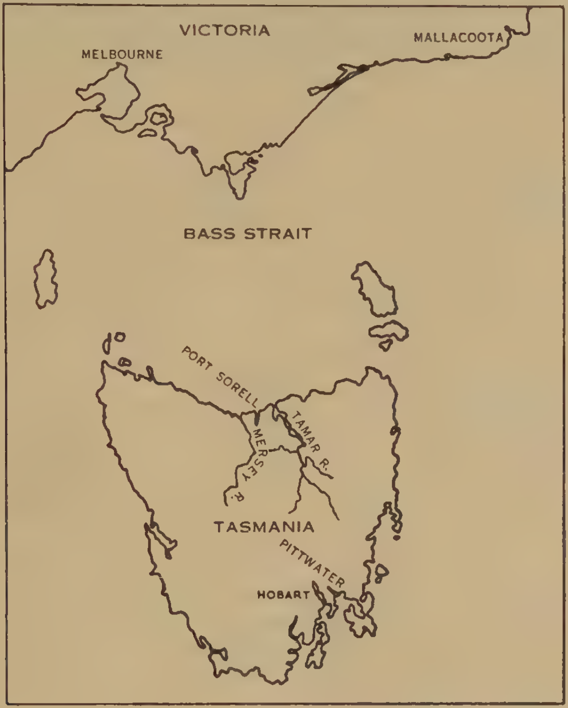
VICTORIA
MELBOURNE
MALLACOOTA
BASS STRAIT
PORT SORELL
TAMAR R.
MERSEY R.
TASMANIA
PITTWATER
HOBART

Fig. 1.—Map of Tasmania and southern Victoria, showing places mentioned in the text.

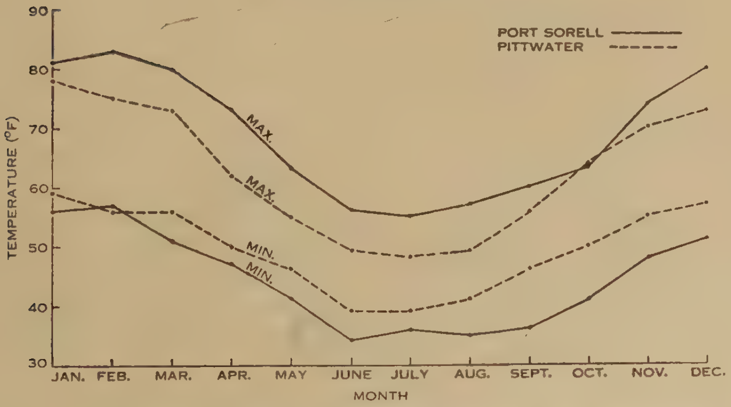

Fig. 2.—The monthly means of the maximum and minimum temperatures at Port Sorell and Pittwater.

In September 1953, the majority of oysters in Pittwater were transferred to Port Sorell. In October 1955 most of the oysters remaining in Pittwater were transferred to Mallacoota Inlet in Victoria (Fig. 1) where conditions were thought to be suitable.

IV. SURVIVAL

The major source of mortality amongst the shipments of 1947 and 1948 was their failure to survive the transfer from Japan to Australia (Thomson 1952). The complete loss of that part of the 1947 shipment placed in Western Australia accounts for the poor survival after 12 months (Table 2).

TABLE 1

SUMMARY OF PACIFIC OYSTER IMPORTATIONS TO AUSTRALIA

Year	No. of Cases	Site	Transport	Period out of Water (Days)	Survival (%)	Survival after 12 Months (%)
1947	28	Oyster Harbour, W.A.	Sea	21	30	0
1947	28	Pittwater, Tas.	Sea	20	30	20
1948	50	Pittwater, Tas.	Sea	20	30	25
1951	5	Pittwater, Tas.	Air	4	99	90
1952	75	Pittwater, Tas.	Air	4	99	90

After the first few years it became impossible to separate the oysters of the four shipments on size as there was complete overlap and the various transfers made it impossible to keep track of the individual trays. Also much mixing occurred by washing from the trays during stormy weather.

TABLE 2

ESTIMATE OF NUMBER OF SPAT IMPORTED AND STOCK OF ADULT OYSTERS REMAINING IN JUNE 1958

Year	Imports Guaranteed Number	Estimated Number	Survival at 12 Months	Estimated Survival 1958	
				Place	Number
1947	672,000	900,000	90,000	Port Sorell	560,000
1948	600,000	850,000	212,500	Mallacoota	74,800
1951	60,000	150,000	135,000	Pittwater	30,000
1952	900,000	2,000,000	1,800,000		
Total	2,232,000	3,900,000	2,237,500		664,800

In Port Sorell a number of oysters died in 1953 following a severe gale which stripped the *Zostera* cover off most of the flats. Rochford (1951) has indicated that the major source of food supply for the oysters is from benthic matter, and Imai *et al.* (1951) have shown that the major source may be the *Zostera* beds. Certainly the condition of the oysters in Port Sorell remained poor for 9 months until the *Zostera* became abundant once more.

In Mallacoota Inlet a large number of oysters was set out on a sand flat which later shifted under the influence of a strong gale and smothered many of them. Apart from these two calamities there was probably a steady mortality from the numerous factors that go to make up natural mortality. Table 2 shows that about a quarter of the oysters alive after 12 months' acclimatization were still living in 1958.

V. Spatfalls

Examination of gonads showed that spawning took place each summer in January, February, or March, except in Port Sorell in 1954 after the loss of the *Zostera* beds when the meats remained dark in colour and watery until late summer. A slight spawning took place in April. In support of this evidence from gonad examination, eye witnesses observed mass spawning in Port Sorell in March 1955, and in January 1956 and January 1957.

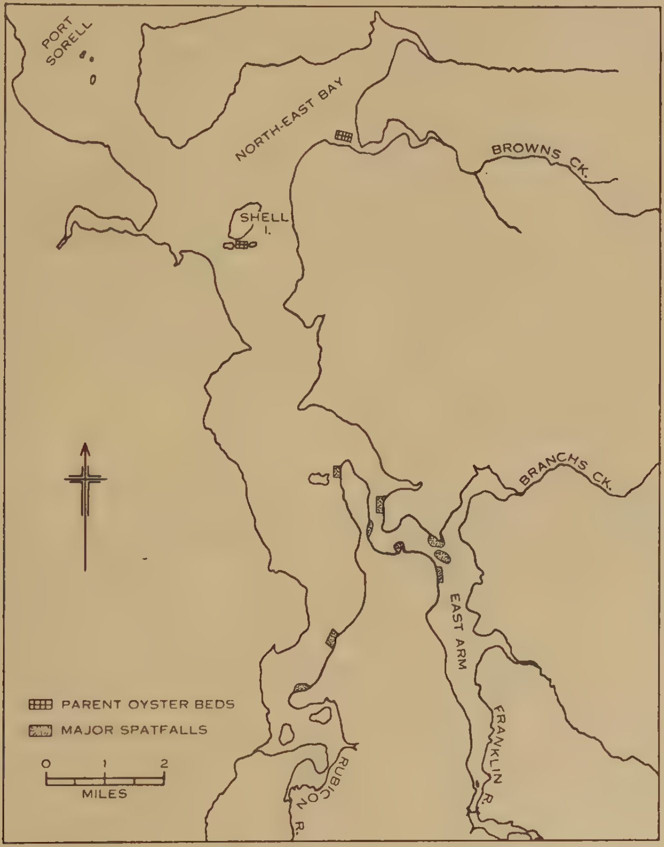
PORT SORELL
NORTH-EAST BAY
BROWNS CK.
SHELL I.
BRANCHS CK.
EAST ARM
FRANKLIN R.
RUBICON R.
PARENT OYSTER BEDS
MAJOR SPATFALLS
0
1
2
MILES

Fig. 3.—Map of Port Sorell, showing the location of the oyster beds and areas of spatfall.

No spatfall has been observed in Mallacoota; a very few spat have been found in Pittwater in most years, but on no occasion in any great numbers. Similarly a few spat were found in Port Sorell each year but in small numbers until in autumn 1958 when larger numbers of spat were located about 7 miles away from the parent stock (Fig. 3). Three distinct size groups of spat were present on these beds, indicating successful spatting in the summers of 1956, 1957, and 1958. The 1956 spat had been believed lost as a heavy flood occurred 2 days after mass spawning was observed. However, either some larvae re-entered the port or other spawnings were successful.

Besides these groups of spat in Port Sorell, spat of the Pacific oyster have now been located in the Mersey River to the west of Port Sorell and in the estuary of the Tamar River to the east (Fig. 1). These can only have reached these estuaries by movement along the coast from Port Sorell. The general movement of water along the north coast of Tasmania is to the east (Australia Pilot 1944, p. 6), but during flood tides inshore on this section of the coast, movement is to the west (loc. cit., p. 139).

TABLE 3

PURCHASE PRICES AND COST OF TRANSPORT OF THE PACIFIC OYSTERS IMPORTED INTO AUSTRALIA

Year	Cases	Price (£)	Freight Japan–Sydney (£)	Freight Sydney–Hobart (£)	Freight Sydney–Perth (£)	Cost per Oyster	
						at Import (*d.*)	at 12 Months (*d.*)
1947	56	63	67	45	190	0·1	0·5*
1948	50	53	†	†			
1951	5	15	205	25		0·4	0·45
1952	75	161	1706	375		0·25	0·3

*Calculated on the basis of the portion set out in Pittwater only. If the cost of those in Western Australia is included the cost would be 1·0*d*.

†No charge was made by the Department of the Army whose ship conveyed the oysters; from Sydney to Hobart the shipment travelled in a divisional research vessel. No cost per oyster has been calculated as the figures would not be comparable with the other years.

The prospects for further spatfalls in Port Sorell seem good, as there has evidently been a regular fall over the last 3 years. The density of the naturally occurring spat is not great, but this is, at least to some extent, due to the lack of clean surfaces on the natural rock, which, although abundant, is frequently covered by slime and mud. Planting of clean cultch in the form of shells, sticks, or fibro-cement slats at the appropriate time (mid to late January) in the spots where spatfall has occurred most heavily should provide an adequate set of spat. The spread of the species to two adjacent rivers indicates that the species has become truly naturalized in northern Tasmania.

VI. GROWTH

The rate of growth for the first 3 years has been given in Figure 3 of the earlier paper (Thomson 1952); this indicates that the annual growth increments become smaller with age. The mean length attained by 5-year old oysters in Mallacoota was 13·7 cm and the range in the sample was from 11·2 to 16·2 cm. The growth of oysters from the later shipments was similar.

VII. Conclusions

It has been shown that a negligible mortality occurred when seed oysters were flown from Japan to Australia. This is an expensive method of transport but in actual fact the costs per oyster were little higher than by sea transport and indeed proved economically sounder because of the improved survival rate (Table 3). No statement is given of the cost of preparing and running the oyster leases as the venture was not carried out as an economic enterprise but on an experimental basis. However, the fact that oyster spat purchased in the native Australian oyster industry costs approximately 0·2*d.* per oyster indicates that this cost of procurement and transport of Pacific oyster spat (Table 3) would be economic. An additional advantage of the Pacific oyster is that for cocktail or fresh consumption it is of suitable size 2 years after setting out, compared with 3–4 years in the case of the Australian Sydney Rock Oyster. For canning purposes the Pacific oyster is better left an additional year.

Spatfalls in Port Sorell and the adjacent rivers suggest strongly that the oyster has become naturalized. In Port Sorell there have certainly been three successive spatfalls whose density was probably limited by the fouling of the natural cultch. Now that the likely areas of spatfall are known, clean cultch material set out just prior to the expected time of spawning would provide a substrate capable of receiving a greater density of spat. As a natural spread has taken place along the coast from Port Sorell, it seems that the Pacific oyster could be cultivated in other northern Tasmanian estuaries.

VIII. References

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THE STATUS OF THE SCHOOL SHARK FISHERY IN SOUTH-EASTERN AUSTRALIAN WATERS

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Summary

The maximum yield of the school shark fishery in south-eastern Australian waters was 4·09 million lb in 1949. The catch has fluctuated since then about a declining trend to 3·18 million lb in 1956.

In 1944, 7·3 hooks were required to catch a shark of mean weight 14·7 lb. In 1956 the number of hooks required was almost doubled: 13·6 hooks were needed to catch sharks of mean weight 13·7 lb; the catch per hook dropped from 2·01 to 0·99 lb. Whereas the catch per boat-month remained relatively stable at 4765 lb for 1944 and 4643 for 1956, the number of hooks used per boat-month increased from 2366 to 4668 hooks in 12 years.

Throughout this period the mean weight of sharks in eastern Bass Strait remained fairly steady (11–13 lb) whereas there was a drop of 3 lb from a mean weight of 17–20 lb in the predominantly mature portion of the stock in western Bass Strait. Fishermen in South Australia have reported a comparable drop in the mean weight of sharks in their catches. During the period 1941–46 there was unrestricted inshore fishing of juveniles and pregnant females with a consequent severe drop in the inshore population. The subsequent decline in the annual total catch is believed to be due not only to a too intensive offshore fishery but also to the resultant reduced recruitment and depressed reproductive potential caused by the earlier destruction of juveniles and pregnant females.

In the data presented in this paper there is evidence that the school shark fishery, which is operating on a single stock of sharks with a slow growth rate, a late sexual maturity, and a low fecundity, shows trends which are suggestive of depletion. Because similar trends in the soupfin shark fishery of California and in the dogfish fishery of British Columbia were followed by depletion, it has been inferred that regulations to protect the vulnerable phases of the life history of the school shark of Australia may be required. Measures for conservation are discussed.

I. INTRODUCTION

The biology, migration, and growth rate of the school shark in south-eastern Australian waters have been described previously (Olsen 1954). The status of the fishery as shown by the catch records, together with the trends they show and their correlation with the biology of the species, are presented in this paper. All weights given represent dressed weights.

There are only meagre catch records from the commencement of this fishery in 1927 until 1943, but thereafter there are available, in Victoria and Tasmania, data which have enabled a detailed study to be made not only of yields but also of the fishing effort and intensity. In the appropriate tables a line has been drawn separating the two periods. There are no such data from South Australia where fishermen are not required to submit returns of fish caught.

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The data used in this study were obtained from the following sources: (1) fishermen's returns and files in the Fisheries and Game Department, Victoria; (2) fishermen's returns and files in the Fisheries Division of the Department of Agriculture, Tasmania; (3) records and files on the shark fishery in the office of the Controller of Fisheries, Commonwealth Department of War Organization of Industry; (4) files of the Division of Fisheries and Oceanography, C.S.I.R.O.; and (5) fish buyers who made their records available, particularly those in South Australia.

When this study of the landings of shark flesh was begun the problem seemed a simple one requiring only the addition of the official figures for each State in order to derive the total catch for the waters of south-eastern Australia. When this was done and the data cross-checked against wartime files there was lack of agreement between the two sets of figures. This was probably due to the diversity of methods used to collect the data and the lack of integration of the various sets of figures from the different sources.

In Tasmania, fishermen were required each month to send returns of *weights* of fish species caught to the Fisheries Division of the Department of Agriculture. These catch records were extracted and sent to the central office of the Controller of Fisheries of the Department of War Organization of Industry, where they were to be integrated with the data from other sources such as the weight of livers received by liver processors. On the other hand, Victorian shark fishermen were required by the Commonwealth Department to forward weekly returns stating the *number* of sharks caught on the amount of gear used in specified grid areas. The Fisheries and Game Department of Victoria required only monthly returns of the *weight* of fish species caught from either the fishermen themselves or the agents they appointed for particular ports. These agents were fish buyers, fishermen, or members of the police force. Some fishermen, although supplying liver to the processors, sent in no returns whatever.

Because of this lack of integration it was necessary to examine personally all the original fishermen's and agents' monthly returns from 1943 to 1956 for both Victoria and Tasmania and correlate these with the data from all other sources. In cases where liver weights only were available the conversion to flesh weight was on the basis of the ratio 10 : 1 flesh to liver; where the number of sharks only was given the mean weight of sharks caught during that month from that port was used to estimate the weight landed. Many errors of interpretation and transposition were corrected and consequently it will be found that figures quoted in this paper may be at variance with previously published official reports.

Before 1933 it was claimed that only gummy shark (*Mustelus antarcticus* (Günther), previously referred to as *Emissola antarctica*), was marketed but it is believed that the distinction between it and school or snapper shark (*Galeorhinus australis* (Macleay)) was neither well understood nor observed. Even now both species are marketed as "flake", the collective trade term for the flesh of these two sharks. The proportion of gummies in the catch varies widely seasonally from port to port, and in some cases the catch may be wholly gummy shark or wholly school shark or varying proportions of each.

II. The Yield of the Fishery

(a) *Victoria*

This State is the centre of the school shark fishery of south-eastern Australian waters. A commercial catch (8921 lb) of shark was recorded for the first time in 1927. The annual total has risen steadily as the fishery extended along the Victorian coast. Within 6 years of its inception 450,600 lb was marketed through Melbourne. There was a steady rise in the catch to a State maximum of 2,772,499 lb in 1949, since when separate and combined landings from Tasmania and Victoria have shown a declining trend (Fig. 1).

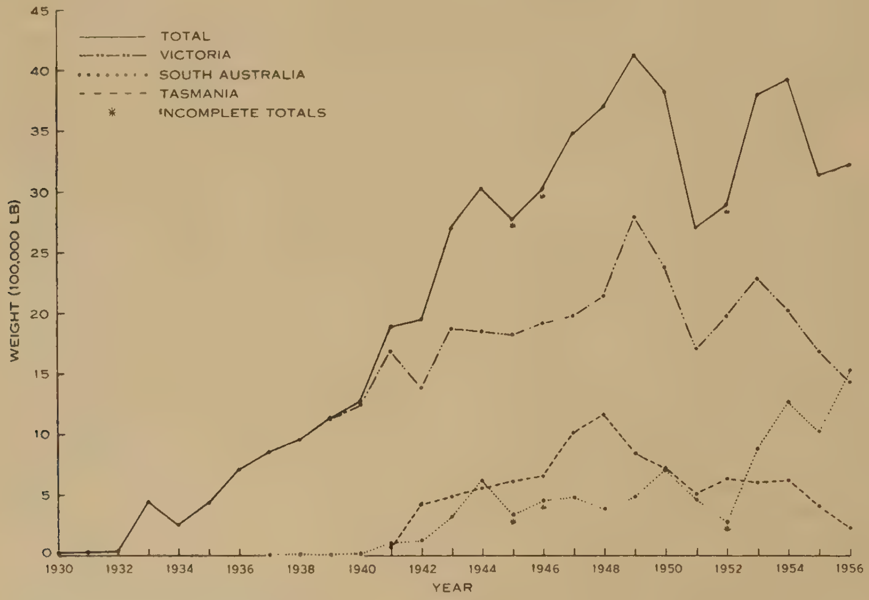

Fig. 1.—Separate and combined total catches for Victoria, Tasmania, and South Australia, 1927–56.

Table 1 shows the total shark catch for both Victoria and Tasmania. The Victorian total is made up of catches of shark landed by the larger shark fishing vessels especially equipped for fishing away from the coast and listed as the offshore catch, and the remainder (from within estuaries, bays, or by boats catching sharks offshore incidentally to their main fishing activities) listed as the miscellaneous catch.

The continued rise in the total catch of this fishery from 1927 to 1940 reflects the increasing demand for the flesh for the fresh fish trade. An even greater stimulus for bigger yields of shark was experienced during the war years, when in response to the national demand for greater food production and for the oil rich in Vitamin A from the livers of the school shark, fishermen made strenuous efforts to catch more sharks. From 1946, the number of offshore shark fishing vessels almost doubled, increasing from 35 to 62 vessels (see Table 7), many of them being newly built, larger vessels, 40 ft and over (see Table 8). Smaller boats were capitalizing also on the increasing demand for both flesh and liver which reached its climax during 1948–49 when every conceivable type of fishing craft that could go to sea caught shark irrespective of its normal fishing. Their catches, therefore, swelled the total landings of shark but because these were not full-time offshore boats their catches were added to the miscellaneous total thus causing it to rise and thereby masking the decline in the catch of sharks from inshore waters.

Table 1

VICTORIAN, TASMANIAN, AND TOTAL SHARK CATCH

(Weight in 1000 lb)

Year	Victoria			Tasmania	Grand Total
	Offshore	Miscellaneous	State Total		
1927	9		9		9
1928	11		11		11
1929	59		59		59
1930	24		24		24
1931	37		37		37
1932	45		45		45
1933	426	25	451		451
1934	248	6	254		254
1935	440	7	447		447
1936	685	32	717		717
1937	809	42	851		851
1938	914	36	950		950
1939	1088	41	1129		1129
1940	1195	54	1249		1249
1941	1650	38	1688	92	1780
1942	1333	47	1380	423	1803
1943	1717	148	1865	498	2363
1944	1585	260	1845	557	2402
1945	1514	299	1813	606	2419
1946	1692	212	1904	654	2558
1947	1696	268	1964	1004	2968
1948	1909	224	2133	1155	3288
1949	2519	254	2773	841	3614
1950	2199	158	2357	725	3082
1951	1536	160	1696	514	2210
1952	1774	177	1951	632	2583
1953	2145	129	2274	605	2879
1954	1907	120	2027	612	2639
1955	1582	83	1665	404	2069
1956	1289	128	1417	236	1653

In 1949 the price of livers reached a maximum and the value of each liver was almost equal to the value of the carcass. Immediately after the collapse of the American liver-oil market in October of the same year, following the dumping of

Japanese shark-liver oil, there was a temporary lowered demand for livers with consequent decreased effort, resulting in a smaller yield. Many Australian shark fishermen changed to other forms of fishing or moved to other fishing ports.

These phases of the fishery are shown by reference to the landings at Lakes Entrance (Table 2). From this port three to four boats, working seasonally from 1936 to 1947, landed annually catches fluctuating around a mean of 35,000 lb. In 1948, 13 boats landed 163,577 lb of shark and in the following year, when another eight boats converted for sharking joined the fleet, 21 boats landed 749,720 lb. The year after the collapse of the liver market 373,784 lb was landed, i.e. half the 1949 total catch, to be followed in 1951 by a catch of only 52,133 lb from 16 boats. Some of the shark boats were converted to trawlers whilst others moved elsewhere. As a result of trawling, more sawshark, *Pristiophorus cirratus* (Latham), were caught and landed. They were called collectively shark, rarely sawshark, and as such were incorporated in the total Victorian shark catch because of the lack of species separation. Because shark was being caught during other forms of fishing it was not possible to make analyses of the Lakes Entrance totals comparable with those of other ports.

TABLE 2

ANNUAL CATCHES FOR MAIN SHARK FISHING PORTS OF VICTORIA

(Weight in 1000 lb)

Year	Portland	Port Fairy	Queenscliff	Westernport	Port Welshpool	Port Albert	Total	Lakes Entrance	Grand Total
1936	25	377	16	22	17	214	671	14	685
1937	88	365	60	23	15	234	785	23	808
1938	79	306	57	52	41	354	889	27	916
1939	63	282	163	120	34	391	1053	36	1089
1940	82	422	135	151	46	330	1166	28	1194
1941	85	465	102	172	213	528	1565	85	1650
1942	89	324	236	27	196	431	1303	29	1332
1943	151	258	490	103	270	432	1704	11	1715
1944	99	196	425	164	292	380	1556	28	1584
1945	162	238	461	69	132	403	1465	48	1513
1946	84	359	343	39	178	641	1644	47	1691
1947	9	470	247	33	177	703	1639	58	1697
1948	9	410	408	65	80	773	1745	164	1909
1949	24	329	414	47	326	629	1769	750	2519
1950	85	282	328	160	451	519	1825	374	2199
1951	63	139	203	171	318	590	1484	52	1536
1952	58	184	302	198	376	551	1669	106	1775
1953	59	217	391	158	645	506	1976	169	2145
1954	56	175	385	207	514	372	1709	199	1908
1955	84	208	260	175	306	383	1416	165	1581
1956	139	159	232	177	143	262	1112	178	1290

However, the increasing proportion of sawshark in the Lakes Entrance catch has served to mask the decline in the catch of sharks in the eastern sector (Table 3), particularly at the traditionally shark fishing port of Port Albert. The latter port also shared throughout the intermittent fishing effort of the Port Welshpool boats which caught school shark during the close seasons and periods of scarcity of crayfish (marine spiny lobster, *Jasus lalandei* (Milne Edwards)).

TABLE 3

ANNUAL YIELDS OF THE THREE SECTORS FISHED FROM VICTORIAN PORTS

(Weight in 1000 lb)

Year	Western Sector	Central Sector	Eastern Sector	Eastern Sector Less Lakes Entrance
1936	403	38	244	230
1937	453	83	273	250
1938	385	108	421	394
1939	345	283	460	424
1940	504	286	404	377
1941	550	273	826	742
1942	414	263	656	627
1943	409	596	714	703
1944	295	589	701	673
1945	401	530	583	535
1946	443	383	866	820
1947	478	280	938	880
1948	419	473	1017	853
1949	353	461	1705	955
1950	367	489	1344	970
1951	202	374	961	908
1952	242	500	1032	926
1953	276	549	1320	1151
1954	231	592	1085	886
1955	293	435	854	689
1956	298	409	582	404

The landings of the boats operating from Queenscliff and Westernport in the central sector in Bass Strait likewise showed a somewhat similar pattern to that of the eastern sector with a gradual rise in landings to 1945, a decline and then recovery within the next 5 years. The higher landings in 1953 were a reflection of the return movements of boats from the eastern sector. Yet despite these changes the total catch did not rise, but fluctuated about the yields of a previous decade.

In the western sector, the total catches from the ports of Portland and Port Fairy have been relatively steady, the effort sustained, and the intensity consistent, yet once again the catches of the previous decade are not being maintained and present totals are lower.

During the decade 1936–45, the ports landing most shark annually were Port Albert, Port Fairy, and Queenscliff. Subsequently Port Albert became the port landing the highest annual catch, its annual total only being exceeded twice, once

Table 4

TOTAL NUMBER OF MONTHS WORKED PER PORT

Period	Port Albert	Port Welshpool	Westernport	Queenscliff	Port Fairy	Portland	State Total (Less Lakes Entrance)
1943, first half	42	15	12	39	35	7	150
1943, second half	48	20	16	37	37	14	172
Total	*90*	*35*	*28*	*76*	*72*	*21*	*322*
1944, first half	44	24	17	38	32	12	167
1944, second half	50	19	22	38	25	11	165
Total	*94*	*43*	*39*	*76*	*57*	*23*	*332*
1945, first half	54	19	10	39	37	9	168
1945, second half	42	16	7	29	23	9	126
Total	*96*	*35*	*17*	*68*	*60*	*18*	*294*
1946, first half	52	14	3	35	65	13	182
1946, second half	54	19	2	25	44	—	144
Total	*106*	*33*	*5*	*60*	*109*	*13*	*326*
1947, first half	58	19	4	24	77	2	184
1947, second half	50	7	—	26	60	—	143
Total	*108*	*26*	*4*	*50*	*137*	*2*	*327*
1948, first half	48	16	7	45	65	1	182
1948, second half	50	10	10	50	58	3	181
Total	*98*	*26*	*17*	*95*	*123*	*4*	*363*
1949, first half	54	33	10	51	62	5	215
1949, second half	43	38	6	35	35	—	157
Total	*97*	*71*	*16*	*86*	*97*	*5*	*372*
1950, first half	41	35	11	34	67	15	203
1950, second half	36	32	12	32	45	6	163
Total	*77*	*67*	*23*	*66*	*112*	*21*	*366*
1951, first half	45	31	23	25	35	8	166
1951, second half	42	32	35	43	28	6	186
Total	*87*	*63*	*58*	*68*	*63*	*14*	*352*
1952, first half	39	38	33	47	55	11	233
1952, second half	47	38	28	38	42	6	199
Total	*86*	*76*	*61*	*85*	*97*	*17*	*422*
1953, first half	36	56	35	52	45	11	235
1953, second half	37	51	28	49	37	5	207
Total	*73*	*107*	*63*	*101*	*82*	*16*	*442*
1954, first half	37	45	22	42	32	11	189
1954, second half	31	48	20	39	49	5	192
Total	*68*	*93*	*42*	*81*	*81*	*16*	*381*
1955, first half	21	32	15	27	37	17	149
1955, second half	37	22	22	35	41	12	169
Total	*58*	*54*	*37*	*62*	*78*	*29*	*318*
1956, first half	25	19	25	27	24	22	142
1956, second half	15	9	26	23	33	7	113
Total	*40*	*28*	*51*	*50*	*57*	*29*	*255*

TABLE 5

MEAN NUMBER OF MONTHS WORKED PER BOAT FOR THE DIFFERENT PORTS

Year	Port Albert	Port Welshpool	Westernport	Queenscliff	Port Fairy	Portland	Mean for State (Less Lakes Entrance)
1943	9·0	8·7	4·6	8·3	10·3	5·2	8·0
1944	9·4	10·7	7·8	10·8	8·1	11·5	9·5
1945	8·7	8·7	4·2	8·5	6·6	6·0	7·7
1946	8·8	8·2	1·6	6·4	6·6	3·2	6·9
1947	9·8	5·2	4·0	5·5	8·0	1·0	7·2
1948	9·8	3·7	5·6	6·3	7·7	2·0	6·9
1949	8·0	8·8	4·0	6·1	6·4	1·6	6·6
1950	8·5	6·7	5·7	4·7	7·4	4·2	6·6
1951	9·6	7·0	5·7	4·8	4·8	4·6	6·1
1952	9·5	7·6	6·1	6·1	7·4	5·6	7·1
1953	10·4	8·2	5·2	5·9	7·4	5·3	7·1
1954	8·5	7·1	8·4	6·7	6·2	5·3	7·1
1955	8·3	6·7	5·4	5·6	7·0	4·1	6·5
1956	8·0	4·7	7·3	8·3	5·7	4·8	6·4

TABLE 6

NUMBER OF MEN WORKING REGULARLY IN OFFSHORE BOATS

Year	Port Albert	Port Welshpool	Westernport	Queenscliff	Port Fairy	Portland	State Total (Less Lakes Entrance)
1943	23	11	13	22	18	11	98
1944	23	12	11	19	19	6	90
1945	28*	13*	9	22	26	8	103*
1946	27	12	9	25	39	10	122
1947	25	14	3	29	45	6	122
1948	23	16	9	43*	42	5	136*
1949	29	21	10	40	39	8	147
1950	26	27	11	42	38*	14*	155*
1951	26	22	29	29	34	9	149
1952	26	28	27	36	34	9	160
1953	18	35	30*	45*	28	8	161*
1954	22	36	14	32	32	8	144
1955	20	22	12	30	28	17	129
1956	13	17	17	18	23	15	103

*Boat working from more than one port.

TABLE 7

NUMBER OF BOATS SHARK FISHING OFFSHORE

Year	Port Albert	Port Welshpool	Westernport	Queenscliff	Port Fairy	Portland	State Total (Less Lakes Entrance)
1943	10	4	6	9	7	4	40
1944	10	4	5	7	7	2	35
1945	11*	4*	4	8	9	3	38*
1946	12	4	3	9	15	4	47
1947	11	5	1	9	17	2	45
1948	10*	7	3	15*	16	2	52*
1949	12	8	4	14	15	3	56
1950	9	10	4	14	15†	5†	55†
1951	9	9	10	14	13	3	58
1952	9	10	10	14	13	3	59
1953	7	13	12*	17*	11	3	62*
1954	8	13	5	12	13	3	54
1955	7	8	5	11	11	7	49
1956	5	6	7	6	10	6	40

*Boat working from more than one port.
†Several boats working from more than one port.

TABLE 8

FREQUENCY DISTRIBUTION OF LENGTHS OF VICTORIAN SHARK FISHING VESSELS

Year	Boat Length (ft)					
	20–30	30–40	40–50	50–60	>60	State Total (Less Lakes Entrance)
1943	1	19	15	4	1	40
1944	1	15	15	2	2	35
1945	2	15	16	4*	1	38*
1946	5	15	17	8	2	47
1947	3	14	19	5	4	45
1948	3	17*	18	8	6	52*
1949	2	18	23	9	4	56
1950	1	15	22†	10	7	55†
1951	4	18	21	10	5	58
1952	1	19	21	12	6	59
1953	4	16	21*	14	7	62*
1954	3	16	18	12	5	54
1955	2	18	19	8	2	49
1956	—	15	18	6	1	40

*Boat working from more than one port.
†Several boats working from more than one port.

by Queenscliff in 1953 and once again by Port Welshpool in 1954 (Table 2). Port Albert can therefore be considered as fairly representative of the trends in Victorian shark fishing ports.

TABLE 9

CATCH PER BOAT-MONTH FOR THE DIFFERENT PORTS

Year	Port Albert	Port Welshpool	Westernport	Queenscliff	Port Fairy	Portland	Mean for State (Less Lakes Entrance)
1943	4802	8355	3693	6454	3577	7196	5295
1944	4044	6800	4209	5590	3439	4296	4688
1945	4196	3782	4048	6777	3973	9028	4986
1946	6049	5406	7852	5721	3292	6449	5046
1947	6512	6801	8151	4944	3427	4311	5009
1948	7891	3069	3837	4293	3330	2283	4807
1949	6486	4588	2947	4812	3395	4732	4755
1950	6737	6734	6976	4972	2518	4040	4987
1951	6782	5053	2999	2980	2202	4484	4215
1952	6404	4942	3244	3549	1900	3418	3953
1953	6930	6028	2509	3875	2646	3686	4471
1954	5471	5527	4934	4750	2166	3470	4485
1955	6605	5663	4734	4189	2672	2902	4454
1956	6539	5090	3473	4637	2795	4785	4357

Initially, Port Albert and Port Welshpool fishermen fished for sharks close inshore (Table 18) along the Victorian coast but by 1943 were extending their operations seawards and 40–60 miles southwards of their home port. In 1944 boats from Port Albert and Port Welshpool made 46 trips due south and 36 trips into the adjacent, more easterly 1° grid squares, i.e. southeast of Port Albert. By 1946 only 29 trips were made into the southerly squares whereas the number to the east and southeast rose to 38 trips. Eventually the number of trips to the south decreased until by 1956 none was made southwards.

TABLE 10

NUMBER OF BOATS OPERATING, SHARKS CAUGHT, AND HOOKS USED

(From special fishermen's returns, Victoria)

Year	No. of Boats	No. of Sharks Caught	No. of Hooks Used	No. of Hooks Used per Shark Caught
1943	32	49,662	389,675	7·84
1944	30	88,307	679,415	7·69
1945	30	57,656	422,487	7·32
1946	28	86,504	604,931	6·99
1947	22	52,940	375,252	7·08
1956	35	79,781	1,017,175	12·7

The extent of the offshore movement away from inshore waters by Victorian shark vessels is reflected in the increase in their registrations to fish Tasmanian waters (Table 13). These waters extend to within 3 miles of Wilson's Promontory (latitude 39°12′ S.). There is evidence from their fishermen's catch returns that the vessels prospected the offshore areas before taking out Tasmanian licences. It was not possible to follow in detail this change in the fishing localities because of the large size of the grid area units (1° squares) in the fishermen's returns.

In 1947, 12 boats (eight Port Albert, two Port Welshpool, and two Westernport fishing boats) were registered and fishing in Tasmanian waters but landing their catches in their home ports in Victoria. By 1948, 21 Victorian shark boats had taken out Tasmanian registrations. This rose to 26 for 1950 through to 1953 before decreasing to 12 in 1956. This extension into Tasmanian waters was being made to counteract the lowered catches from their own Victorian waters. The trend for Port Albert is shown in Table 9 where the catch per boat-month fell for the first 3 years before recovering in 1946 and being maintained at an apparently steady level thereafter. The sudden rise in the Port Albert catch per boat-month of 4196 lb in 1945 to 6049 lb the following year and then to 7891 lb in 1948 reflected the change in methods from an inshore manual fishery to a mechanized offshore one in eastern Bass Strait. The number of hooks used per catch decreased, i.e. fishing improved (Table 10) with these changes in the fishery.

Tables 4–10 summarize data for all ports (except Lakes Entrance, for the reasons stated earlier). Table 4 presents the total number of months (in two 6-monthly periods, January–June and July–December) worked per port during 1943–56; Table 5, the mean number of months worked per boat for the different ports; Table 6, the number of men working regularly in offshore boats; Table 7, the number of boats shark fishing offshore; Table 8, the frequency distribution of lengths of Victorian shark fishing vessels; Table 9, the catch per boat-month for the different ports; Table 10, the number of boats operating, sharks caught, and hooks used according to special fishermen's returns in 1943–47 and 1956.

During the 14-year period 1943–56 (Table 4), fishing activity was greater in the summer–autumn period eight times, during the winter–spring period three times, and spread more or less evenly throughout the year during the remaining three years. Table 11 shows that the number of trips from each of the ports for each half year decreased in the spring and increased in the summer–autumn half of the year during the crucial period (1944–47) when the fishery moved from inshore to offshore waters. From Table 9 it would seem that in some cases the catch per boat-month for any one port was disproportionately high (e.g. Westernport 1947), but if reference is made to Tables 4 and 7 it will be seen that only one boat in the year in question was working for only 4 months from that port and hence such results are not so truly representative as for a more typical port such as Port Albert.

Because of the incompleteness of many fishermen's returns it was only possible to obtain detailed analyses on gear used and effort for 1944 and 1956 for some boats at each of the different Victorian ports. These years are representative of the two different phases (inshore and offshore) in the development of the shark fishery; the State total catch per boat-month for 1944 was 4688 lb, for 1956 it was 4357 lb.

During 1944, seven of the ten Port Albert boats landed 30,412 sharks weighing 341,550 lb from 186,600 hooks. Twelve years later, in 1956, five boats, three of which operated in 1944, landed 20,338 sharks weighing 261,575 lb from 279,200 hooks. It required six hooks to catch one shark of mean weight 11·23 lb in 1944 whereas 13·7 hooks were required for one shark of mean weight 12·86 lb in 1956. The slight increase in mean weight is considered to be attributable to the present market discouragement of small fish and the operation of a legal minimum size.

TABLE 11

MEAN NUMBER OF TRIPS FOR EACH HALF YEAR MADE BY OFFSHORE SHARK FISHING VESSELS 1943–47 AND 1956

Period	Port Albert	Port Welsh-pool	Western-port	Queens-cliff	Port Fairy	Port-land	Mean
1943, second half	14	8	5	14	11	9	11
1944, first half	13	9	4	9	12	18	11
1944, second half	13	10	3	10	6	9	9
Total	*26*	*19*	*7*	*19*	*18*	*27*	*20*
1945, first half	8	10	6	9	11	19	9
1945, second half	15	7	5	8	8	8	9
Total	*23*	*17*	*11*	*17*	*19*	*27*	*18*
1946, first half	15	14	15	9	12	8	12
1946, second half	10	7	8	6	5	12	7
Total	*25*	*21*	*23*	*15*	*17*	*20*	*19*
1947, first half	11	13	12	5	11	—	10
1947, second half	8	4	—	4	8	—	7
Total	*19*	*17*	*12*	*9*	*19*	—	*17*
1956, first half	15	8	11	9	7	6	9
1956, second half	11	12	7	4	5	2	6
Total	*26*	*20*	*18*	*13*	*12*	*8*	*15*

If reference is made to Table 12 it will be seen that at Queenscliff, Port Fairy, and Portland the average weight of the sharks caught has dropped. Sharks in the eastern sector of Bass Strait have always been smaller than elsewhere (Olsen 1954, p. 381). After 12 years the fishery had become dependent on fish of lower average weight than formerly. The figure (14·7 lb) for the mean weight for the State is 1 lb lighter in 1956 than in 1944 but the 1956 figure for the mean weight is biased by the rise in the proportion of the catch from the western sector.

In 12 years the number of hooks per shark caught has doubled at all ports except Port Fairy. The average for the State shows an almost twofold increase from 7·3 to 13·6 hooks per shark. This result is exemplified by reference to Table 12 which shows that 2366 hooks were used for a catch of 4765 lb per boat-month in

Table 12

COMPARATIVE CATCH ANALYSES FOR VICTORIAN PORTS FOR 1944 AND 1956

Port	Total No. of Boats for Port	Total Catch for Port (1000 lb)	No. of Shark Boats	No. of Sharks Caught	No. of Hooks Used	Wt. of Shark Landed (1000 lb)	Total No. of Months Worked	Mean No. of Months Worked	Shark Mean Weight (lb)	Hooks/ Shark	lb/ Hook	Catch/ Boat-Month (lb)	Hooks/ Boat-Month (lb)
						1944							
Port Albert	10	380	7	30,412	186,600	342	74	10·5	11·23	6·1	1·83	4615	2521
Queenscliff	7	425	5	20,636	118,830	356	58	11·6	17·26	5·7	2·99	6142	2048
Port Fairy	7	196	6	10,218	139,985	176	49	8·1	17·18	13·7	1·25	3583	2856
Portland	2	99	2	4,831	37,275	99	23	11·5	20·45	7·7	2·65	4296	1620
Total	26	1100	20	66,097	482,690	973	204						
Mean								10·2	14·7	7·3	2·01	4765	2366
						1956							
Port Albert	5	262	5 (3)*	20,338	279,200	262	40	8	12·86	13·7	0·94	6539	6980
Queenscliff	6	232	6 (3)	16,420	210,100	232	49	8·1	14·12	12·79	1·10	4741	4287
Port Fairy	6	159	6 (4)	12,457	138,550	153	51	8·5	12·24	11·12	1·10	2990	2716
Portland	9	139	9 (–)	7,881	161,075	139	29	3·2	17·6	20·43	0·86	4785	5554
Total	26	792	26 (10)	57,096	788,925	786	169						
Mean								6·5	13·7	13·61	0·99	4643	4668

*Figures in brackets indicate number of boats which operated also in 1944.

1944 whereas 4668 hooks per boat-month were used to catch 4643 lb in 1956. Double the amount of gear, i.e. effort, was used in the fishery to make the same catch 12 years later. Thus the seeming stability of the State mean catch per boat-month (Table 9) through to 1956 does not present a true picture, the decline being masked by the lack of information about the amount of gear used. The figure for 1956 shows that the value of 4357 lb per boat-month is not comparable with that for 1944 when the amount of gear used is considered, but actually is only half the stated figure, i.e. about 2170 lb per boat-month, for the same amount of effort.

(*b*) *Tasmania*

The shark fishery in Tasmania differs markedly from that of Victoria in that there is not so much specialization of effort. Fishermen do not limit their efforts to the catching of one species, but rather catch species either readily available or seasonally abundant. Thus a crayfishing vessel will catch shark when crayfish are not readily available or barracouta, *Thyrsites atun* (Euphrasen), when this fish is present in quantity. Hence it has not been possible to analyse the records of the Tasmanian shark fishery to the same extent as was done with those of the Victorian shark fishery.

Nevertheless similar trends are evident as indicated by the graph of the Tasmanian catch (Fig. 1). Initially the fishery was an inshore one but by 1946–47 it had moved out into offshore waters. Hence the sudden rise in the 1947 total Tasmanian catch. The details of the weight changes (Table 12) apply equally well to Tasmanian fishermen because of the overlap in fishing areas in Bass Strait and because of the migratory nature of the one stock of school shark (Olsen 1954). In Appendix II, Table 21, are shown the landings for eight different areas (see Appendix I) together with those from Victorian fishermen registered to fish Tasmanian waters.

Because of the manner in which catches were recorded in Victoria and Tasmania there has been an erroneous appraisal of the size of the shark fishery in south-eastern Australian waters owing to the registration in Tasmania of fishermen domiciled in Victoria. Fishermen registered in Tasmania are required to forward monthly returns showing the weight and number of the fish species caught. Although the Victorian-domiciled fishermen registered in Tasmania sent their fish returns to Tasmania, agents appointed at certain ports by the Victorian Department of Fisheries and Game listed the landed catches of these men with those of the Victorian registered fishermen from these ports and forwarded them to Melbourne. These landings were subsequently entered in the Victorian total as the total catch landed at that particular port. Thus the one catch was recorded twice and as such appeared in the combined totals of the two States. When the present author discovered this anomaly it was corrected by both departments concerned and a system of recording was evolved to prevent such errors in future. The column in Table 13 headed Victorian fishermen registered to fish in Tasmanian waters is included in case it is necessary at any time to reconcile these figures with those previously published in official reports.

Table 13 shows the increase in numbers in Victorian vessels and men registered to fish in Tasmanian waters. However, these figures have not been used in the preparation of the histogram (Fig. 2) comparing the percentage distribution of sizes of fishing vessels catching sharks in Tasmania during the period 1943–56.

TABLE 13

NUMBER OF VICTORIAN VESSELS AND MEN REGISTERED TO FISH IN TASMANIAN WATERS

Year	No. of Fishing Boats Registered	No. of Men Registered
1943	2	6
1944	2	6
1945	3	10
1946	3	10
1947	12	31
1948	21	54
1949	19	48
1950	26	73
1951	26	75
1952	26	76
1953	26	74
1954	24	69
1955	18	50
1956	12	36

The lengths of these vessels have been used in the preparation of Table 8. It shows that despite the changes which occurred during the period 1948–50 there is still the same proportion of the different sizes of vessels catching shark although there is a reduction of four-fifths in their total number. Appendix II shows that several

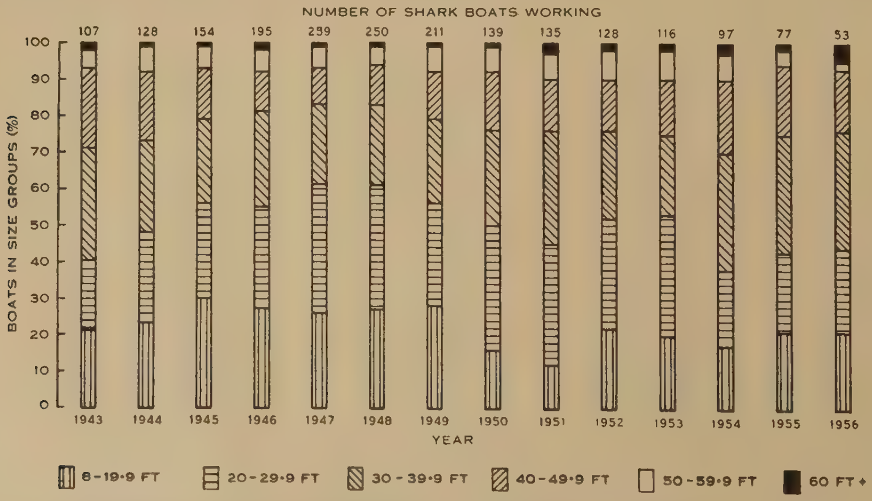

Fig. 2.—Distribution of sizes of Tasmanian fishing vessels expressed as percentage of total number registered.

areas, particularly areas 1, 4, and 8, show a marked diminution in their yields and area 7 is the only one whose yields have been consistent throughout; even this yield shows a decreasing trend over the past 6 years.

(c) *South Australia*

The data used in the preparation of Table 14 have been obtained from a number of sources; from fishermen, fishermen's cooperatives, buyers and their agents, all of whom made available for study their logs, their catch records, and their shark intake records respectively. So far as the author is aware this table lists the most complete set of figures of shark landings available from South Australian sources.

For the purpose of analysis, three separate fishing areas have been recognized: (1) the south-east area embracing all the ports from Port MacDonnell to Kingston, (2) the west from Port Lincoln along the coast to Ceduna, (3) the central area encompassing Kangaroo Island and all the remaining ports not included within the limits of the south-east and west areas (see Appendix I). Although boats may fish within the waters of other areas, the port of landing is credited with the catch. For instance, fish caught near Kangaroo Island in the central area were added to the west area total if landed by a Port Lincoln boat at its home port.

From Table 14 it will be seen that the main catches were made initially in the south-east area and it was not until 1944 that shark fishing started on the west coast. Shark were always caught for crayfish pot bait and, from 1937 until this virtually ended about 1944, limited quantities were sold through the Adelaide Fish Market (Table 15). In 1947, the manager of the Market advised the author that practically no shark was sold from 1944–47. The decline in sales through this source followed the establishment of refrigeration plants by private buying agencies at the different ports.

In common with the other States the demand for the school shark liver increased in 1942. From then until early 1945 fairly complete records of the number of sharks caught and of their weight and liver yields were compiled for the Fish Liver Oil Committee of the Department of War Organization of Industry. There was a transition period after 1945 during which the catch records of shark were incomplete but, at least, those available do show the trends in the fishery. From 1945 to 1952 the shark catches in the south-east dropped considerably but crayfish landings increased fourfold because the fishing effort of the shark boats was transferred to the accumulated stock of crayfish built up during the war years.

From 1950 the fishing fleet out of Port Adelaide tended to concentrate more on shark because of the difficulty of procuring materials for making crayfish pots and because the returns from sharking were more lucrative. The slump in the American liver oil market did not affect South Australian fishermen quite so noticeably because the crayfishery in the south-east was able, at that time, to absorb those who had been engaged in shark fishing.

In 1952 the transfer of several shark fishing vessels from Port Fairy and Portland (Victoria) to Port Lincoln resulted in increased annual yields from the west area. Although the total landed catch in this area exceeded 1 million lb in 1954, dropped to 861,080 lb the following year, and then rose to 981,491 lb in 1956, it was at the price of longer voyages, more gear used, and higher operating costs. In mid 1957 some shark fishermen were forced out of the industry because of lowered monetary returns. The catch from the fishery for the first half of 1957 was considerably less than that for the comparable period in 1956.

TABLE 14

SHARK CATCH BY AREAS, SOUTH AUSTRALIA

(Weight in 1000 lb)

Year	South-East	Central	West	Total
1937	7			7
1938	8			8
1939	3			3
1940	22			22
1941	106			106
1942	127			127
1943	336			336
1944	549	13	58	620
1945	211*	13	121	345*
1946	116*	32	311	459*
1947	266	22	196	484
1948	174	11	202	387
1949	166	88	231	485
1950	434	115	163	712
1951	93	177	198	468
1952	57*	41*	188*	286*
1953	206	—	680	886
1954	224	1	1030	1255
1955	129	45	861	1035
1956	443	107	981	1531
1957	293†	182†	421†	896†

*Incomplete totals.
†Six months only.

The catches of representative boats in the south-east area during 1942–44 have been analysed and the results are shown in Table 16. No such data were available from similar South Australian sources a decade later but, in April 1953, the C.S.I.R.O. Fishery Research Vessel *Derwent Hunter* made a special cruise for shark data into South Australian waters as far west as Nuyts Reef, Fowler's Bay, at the head of the Great Australian Bight. An analysis of the 218 school sharks caught and examined during this cruise gave the following results: weight, 4652 lb; liver, 598·4 lb; mean weight of fish, 21·3 lb; mean weight of liver, 2·7; ratio flesh : liver, 7·7. These results show that up to the period of the research cruise the composition of the catch had not changed.

An analysis of the sizes of the sharks caught by the research vessel and measurements taken of catches of commercial vessels showed that if all fish over

135 cm were considered mature, then the stock as fished in April 1953 was composed of approximately 20 per cent. immature fish. This condition must have held throughout the course of the South Australian shark fishery from 1938 until 1953 or 1954, for during this time the mean weight of the sharks remained much the same and the ratio of flesh to liver was relatively stable. The ratio of the yield of flesh to liver over the same period was approximately 10 for Victoria and 7 for South Australia, i.e. the average size was larger in the latter State.

TABLE 15

SALES OF SHARK THROUGH ADELAIDE FISH MARKET

Year	Weight (lb)
1937–38	6,800
1938–39	7,500
1939–40	3,200
1940–41	21,800
1941–42	106,351

In eastern Victorian waters between 1944 and 1956 the average weight of shark was 12–14 lb (Table 12). It is known that the size composition of school sharks varies from a smaller size in eastern Bass Strait to a larger size in western Bass Strait (Olsen 1954). From the above tables there is evidence that the larger sharks were fished in South Australian waters. The dressed weight of shark carcasses in South Australia averaged 20–21 lb until 1953, since when there has been an obvious decrease in both weight and size of sharks caught (cf. Portland, Table 12). It is a corollary that, in the last two years, increased numbers of lighter weight, i.e. smaller-sized, sharks have had to be caught not only to maintain but to increase

TABLE 16

ANALYSIS OF THE CATCHES IN SOUTH-EAST AREA FROM FILES OF THE LIVER OIL COMMITTEE

Port and Year	No. of Fish	Weight (lb)	Liver (lb)	Fish Mean Weight (lb)	Liver Mean Weight (lb)	Flesh : Liver Ratio
Beachport						
1942	5344	112,758	16,353	21·1	3·1	6·9
1943	6883	148,496	20,603	21·6	3·0	7·2
1944	8599	173,614	23,190	20·2	2·7	7·5
Robe						
1942	708	15,294	2,055	21·6	2·9	7·4
1943	1000*		2,762		2·7	
1944	3263†		8,637		2·6	

*December. †January.

the State total catch of sharks to 1½ million lb in 1956. The highest monthly landings of shark are made during the period March–May as shown by the total monthly catches over the period 1947–56 (Fig. 3).

Prior to about 1945 the catching rate of gear in the south-east area was of the order of 10 per cent. but by about 1947 the rate had decreased by at least half. The larger sharks were mostly caught inshore, i.e. within 12 miles, but further seawards nearer the edge of the continental shelf, the sizes of the sharks tended to decrease. For that reason the fishermen operated inshore before working seawards later. They attempted to maintain their catch average at the highest possible figure.

Much the same sequence of events occurred in the west area except that there was a lag of about 5 years behind that of the more heavily fished south-east area.

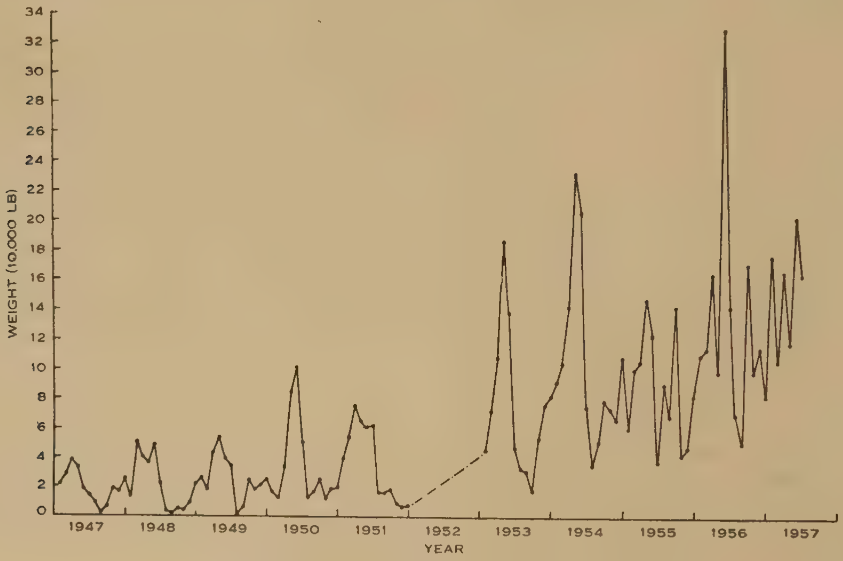

Fig. 3.—Monthly total catches in South Australia, 1947–56.

In the west area the degree of exploitation was lower initially and hence the yield per unit of effort remained higher for a longer period, and was maintained at the rate of about ten fish per 100 hooks until after 1951 when it likewise declined to about five fish per 100 hooks and showed the same trend as the south-east area.

The Port Lincoln fishermen noticed that slightly more juvenile sharks were being caught from 1952 onwards. It could have been due to the increasing tendency of fishing further seawards and hence encountering more of the smaller sharks as in the south-east area. However, conditions in the west area differ from those in the south-east where the continental shelf is much narrower, and what applies there probably does not hold elsewhere. The number of juveniles present in the early years from 1952 were not sufficient to alter appreciably the average dressed weight of the carcasses (cf. results of cruise of F.R.V. *Derwent Hunter*). Fishermen from the south-east area reported that from about 1955 the average dressed weight of shark had dropped to 16–17 lb (cf. Portland 1956, Table 12). Increasing numbers of smaller sharks are now present in their catches. These observations support the evidence from the 1956 catch statistics of western Victorian ports and the returns of tagged sharks from South Australian waters.

In April 1953, 204 sharks were tagged and released offshore in South Australian waters. Up to September 30, 1957, 22 tags (10·8 per cent.) had been recovered, five from waters outside the State. At the time of tagging, 43 sharks (21 per cent.) were less than 135 cm and therefore were considered immature. Of the 22 sharks recaptured, five were less than 135 cm at release but by the time they were caught again, 6 months to 4 years later, all but one had exceeded that length. The recovery rate of 10·8 per cent. for South Australia is higher than that obtained for double tagged sharks (Olsen 1953) in all other waters. From a study of these recovery rates (Table 17) it can be inferred that the fishing intensity is high on the South Australian portion of the stock of school sharks.

Table 17

RECOVERY OF SHARKS TAGGED IN WATERS OUTSIDE SOUTH AUSTRALIA

Year	No. Tagged	Recoveries	Percentage
1950	1802	112	6·2
1951	1087	103	9·5
1952	161	10	6·2
1953	207	15	7·2
Total	3257	204	6·3

III. Discussion and Conclusions

Female school sharks require 10–12 years to reach sexual maturity and bear only about 30 young at each gestation (Olsen 1954). Such slow growth rate and low fecundity make the school shark vulnerable to heavy fishing. For these reasons the course of a shark fishery should not be compared with that of commercial food fishes, which have an enormous reproductive potential and a relatively fast growth rate. It should be compared rather with the fisheries for sea mammals, such as whales and seals (Thompson 1947–53; Kenyon and Sheffer 1955). The Australian school shark fishery is also comparable with that for elasmobranchs in other parts of the world. Its course is somewhat similar to the fishery on the American soupfin shark, *Galeorhinus zyopterus* Jordan & Gilbert. These species have a comparable growth rate and an average of 30 young at each gestation. The fisheries had modest beginnings; that of the soupfin from 1930–36 yielded a little over half a million pounds of flesh annually, but in 1938 the catch rose eightfold to 7·5 million pounds. This sudden rise followed the discovery, the previous year, that the soupfin shark liver oil was the richest source of high potency Vitamin A oil available in commercial quantities. In 1939 the yield rose to 9·2 million pounds, dropped below 8 million pounds during the next two years, and then declined rapidly to its former level by 1944 (Ripley 1946). The increased catch of soupfin from 1938 to 1941 meant a great intensification of fishing effort by about 600 boats, which the stock was unable to withstand, and it declined rapidly. A somewhat similar effect was produced on the stocks of the west coast dogfish, *Squalus suckleyi* (Girard), in British Columbia waters (Barraclough 1948).

The history of the Australian school shark fishery shows a slower development because of lesser fishing effort. Except for the earlier history of the fishery from 1929–34 (Fig. 1), the weight of the annual catch of sharks from south-eastern Australian waters increased more or less steadily to a maximum in 1949. In 1947, some 20 years after the fishery began, the maximum number of boats operating offshore in Victoria and Tasmania reached only 304 and fishing intensity was not equally heavy throughout its range as had been the case for the soupfin, which was fished over the whole of its range within the continental slope of North America.

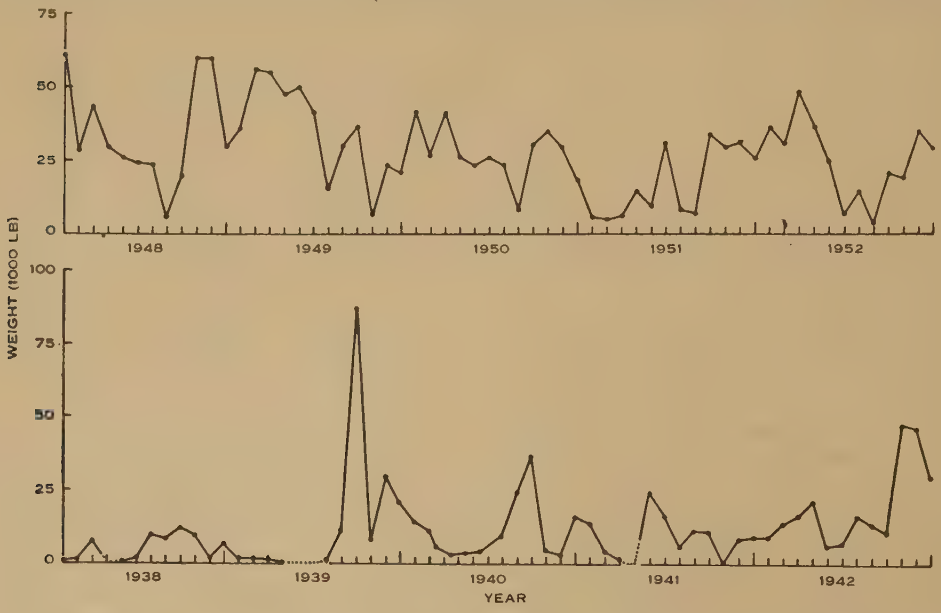

Fig. 4.—Monthly catches for Queenscliff area for the 5-year periods 1938–42 and 1948–52.

The increased demand in Australia for greater production of fish for fresh food and an oil rich in Vitamin A to replace overseas oil supplies cut off by hostilities during World War II, and the lessened availability of large sharks in the inshore sheltered waters of Victoria because of increased fishing intensity, led to the development of an offshore fishery. Fishermen in Tasmania and South Australia were encouraged to fish the resource hitherto untapped.

The following more detailed description of the Australian fishery discusses the earlier inshore fishery and its change to the present offshore fishery. The fishery was inshore until about 1942, the biggest catches being landed in the spring months of September and October (Fig. 4), when the fishery concentrated on the pregnant females as they moved inshore to drop their young. Queenscliff was one of the few Victorian ports in which boats were built specifically for shark fishing and, by

1948, an extended all-year-round offshore fishery had developed using these new larger boats. A comparison of the monthly catches landed at Queenscliff during the two 5-year periods, 1938–42 and 1948–52, shows clearly the change from a spring inshore fishery to an offshore fishery. This evidence is supported by an analysis of replies to a questionnaire sent in 1945 by the Senior Inspector of Fisheries, Victoria, to shark fishermen of that State. A similar questionnaire was sent in 1951 to the same fishermen by C.S.I.R.O. Table 18 gives a summary of the replies received from ten fishermen and indicates the increase in distance travelled to fishing grounds and the increase in the number of hooks used, showing the change in the fishery in Victorian waters in that 6-year period.

TABLE 18

EXTRACT OF ANSWERS TO QUESTIONNAIRES, 1945 AND 1951

Port	Period of Years Spent Shark Fishing	Average No. of Miles to Fishing Area			Average No. of Hooks Used		
		Before 1940	1945	1951	Before 1940	1945	1951
Port Albert	24	7	60	60	<1200	1200	2000
Port Albert	26	4	—	80	600	1400	2400
Port Albert	21	5	—	60	<1200	1200	2400
Port Albert	30	1	—	60	400	1000	2200
Queenscliff	19	46	60	70	<1000	1000	800
Queenscliff	21	40	70	70	500	1500	1600
Queenscliff	24	17	75	75	<1240	1240	1500
Queenscliff	17	60	75	75	800	1300	1400
Port Fairy	21	30	30	40	—	800	1000
Port Fairy	13	—	6	35	< 900	900	1200

TABLE 19

CATCH RECORDS FOR EARLY PERIOD OF SHARK FISHING AT STANLEY, TASMANIA

Year	No. of Trips	Total No. of Hooks	No. of Sharks	No. of Hooks per Shark	Average Distance Travelled from Base to Fishing Area	No. of Hook-Miles per Shark
1942	3	600	292	2·0	3·0	6
1944	14	8000	1688	4·7	6·3	29
1946	5	4400	861	5·1	18·0	91
1947	8	6100	687	8·9	10·6	94
1948	3	3000	470	6·4	24·0	153

In Table 19, prepared from the logs and catch records of a fisherman from Stanley, Tasmania, it can be seen that initially virgin grounds were fished inshore, but later fishing activity was extended further north-westward where fishing was better and where less gear, that is a smaller number of hooks per shark, was used. This development is similar to that shown for Victoria (Tables 10, 12, and 18).

Although fishing operations in offshore areas were developing, the fishery on the juvenile groups continued. Figure 5 gives the annual yield of shark from Port Phillip Bay and indicates that the catch was increased threefold from 1942 to 1944, sustained at that level for another year, and then fell slowly at first and later precipitately.

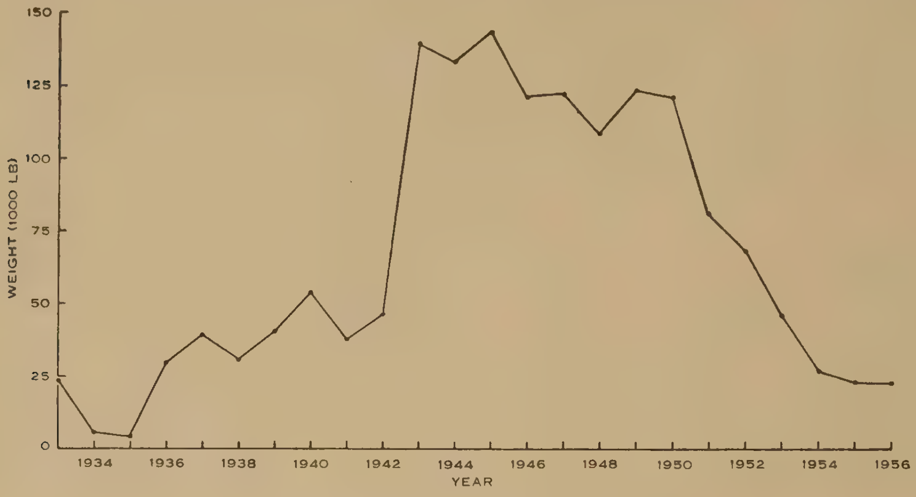

Fig. 5.—Catch of shark, Port Phillip Bay, 1933–56.

This decline occurred not only in Victorian nursery areas, but in Tasmanian bays and estuaries. In Tasmania, at both Pittwater and Port Sorell (350 miles apart), juveniles were harder to catch for tagging experiments (Table 20). The temporary improvement in the catch of 1951 was due solely to changes in methods and times of fishing. Though the Tasmanian and Victorian offshore catches were still rising to their respective maxima in 1948 and 1949 (and the South Australian in 1956), the cause of the declining trend after 1950 can be assigned to the intensive fishing of juveniles when for the three years 1943–45 in Port Phillip Bay alone 60,000 young sharks, averaging 2 lb in weight, were caught annually. It is the opinion of the present author

TABLE 20

NUMBER OF LINE-HOURS TO CATCH ONE JUVENILE SHARK (JANUARY–MARCH) IN TWO ESTUARIES IN TASMANIA

Year	Port Sorell	Pittwater
1948	2·57	0·73
1949	2·11	4·73
1950	8·1	9·75
1951	20·86	4·27
1952	—	8·9

that this unrestricted fishing of the juveniles in the bays and estuaries, and the catching of pregnant females as they moved inshore to pup, may well have decreased the potential breeding portion of the stock and thus affected adversely the offshore catch of adults.

Fishermen, attempting to meet this decline, improved their methods using echosounders, ice boxes, refrigeration, and automatic line haulers. The automatic haulers enabled the fishermen to work 2000–2500 hooks on consecutive days. Sometimes three and four shots of gear were made on a trip. Whereas formerly boats made between 20 and 30 trips per year, shot their gear once, hauled it and returned to port, more recently they used the maximum amount of gear that they could work effectively, and shot it at least twice, thus doubling the number of hooks used to catch the same weight of shark as formerly (Table 12).

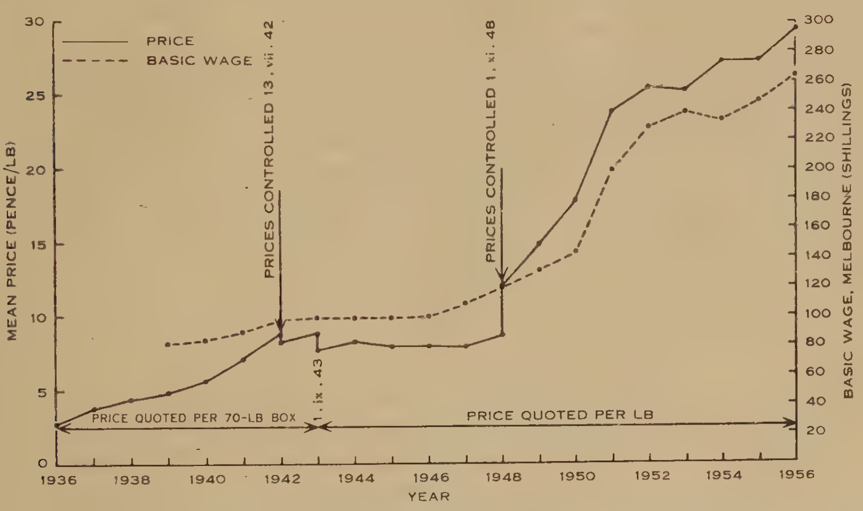

Fig. 6.—Mean price paid for school shark, Melbourne Market 1936–56 (by courtesy of the Superintendent of Markets, Melbourne).

There is a similarity, which may be significant, in the shape of the curves of the monthly yields for Queenscliff in 1938–42 (Fig. 4) and for that nearly 10 years later for South Australia, 1947–52 (Fig. 3). This similarity is not confined to the first period of the curves but extends also to the second period. The initial lag period of nearly 10 years is halved in the comparison between the second set of curves, i.e. 1948–52 for Queenscliff with 1953–57 for South Australia. These curves indicate that at first the fishery was seasonal but later became more intensive with the monthly yields fluctuating. If this similarity is real, then it can be expected that the shark fishery in South Australia will follow a similar pattern to that out of Queenscliff (Table 12). The number of boats may be expected to drop (Table 7) and those remaining in the fishery will work longer because of the greater distances they will have to travel, yet the total catch may be expected to continue to drop (Table 2).

The price per pound of shark flesh has increased threefold since 1946, but this increase has little relation to the catch of shark. Figure 6 shows the average price paid to the fishermen from 1936 to 1956. It is suggested that this price has followed inflationary economic trends as can be seen by examining the graph of the Australian Federal basic wage which has been plotted on Figure 6. Thus market prices cannot be used in the analysis of the fishery.

The data presented and discussed in this paper do not show that the population of school shark is depleted. However, the author considers that trends in the fishery, although developed over a longer period, are similar to those which resulted in the depletion of the soupfin shark fishery, and he considers the situation sufficiently urgent to merit the discussion of conservation measures. Because of the nature of this fishery, and the biology of the stock on which it depends, any short-term remedial measures for arresting the decline in the fishery would impose an unnecessarily severe hardship on the men engaged in the fishery, so such measures are not discussed.

The evidence presented in this paper indicates a serious decline in the catch of juvenile sharks (Table 20); it is therefore considered that the imposition of a legal minimum total length of 36 in. would protect the juvenile sharks while inshore. An even more effective protection to the species would be given by declaring the nursery areas and restricting or prohibiting fishing in those areas. It has also been stressed that the fishery has concentrated on the pregnant females, so a closure of inshore waters during October to December would protect them during this vulnerable phase.

In this paper evidence has been given of a decline in total catch (Table 1), a reduction in the number of boats operating in the fishery (Table 7 and Fig. 1), a decrease in catch per hook (Table 12), a decrease in the mean weight of sharks (Table 12), an increase in gear carried by each fishing boat, discussed as hooks per boat-month (Table 12), and the change from an inshore to an offshore fishery involving increases in distances travelled from port (Tables 13, 18, 19). In view of this evidence the author has felt justified in discussing measures to conserve the stocks in order to maintain a maximum steady yield.

IV. ACKNOWLEDGMENTS

The help of Mr. A. D. Butcher, Director, and members of the staff of the Fisheries and Game Department, Melbourne, and Mr. L. St.Leger, Secretary, and members of the Fisheries Division, Department of Agriculture, Hobart, is acknowledged.

Grateful thanks are due to the many buyers interviewed in the fishing industry in South Australia who gave access so readily to their confidential trading documents, thus permitting an assessment of the catch of sharks in that State.

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Appendix I

PRINCIPAL FISHING PORTS

(*a*) *Victoria*

Main Fishing Ports	*Subsidiary Ports*
Portland	—
Port Fairy	Warrnambool
Queenscliff	Apollo Bay, Lorne, Torquay, Barwon Heads, and Ocean Grove
Westernport	San Remo, Newhaven, Flinders, Rhyll
Port Welshpool	Port Franklin, Foster
Port Albert	—
Lakes Entrance	Mallacoota, Marlo

(*b*) *Tasmania*

Fishing Area	*Approximate Limits*	*Main Port*
1	Cape Sorell–Frederick Henry Bay	Hobart
2	Frederick Henry Bay–Marion Bay	Dunalley
3	Marion Bay–Cape Lodi	Triabunna
4	Cape Lodi–Cape Naturaliste	St. Helens
5	Cape Naturaliste–West Head	Bridport
6	West Head–Table Cape	Devonport and Wynyard
7	Table Cape–Cape Sorell (including King I.)	Stanley
8	Furneaux Group	Lady Barron

(*c*) *South Australia*

South-east area:	Port MacDonnell, Beachport, Robe, Kingston.
Central area:	Victor Harbour, Port Adelaide, Kingscote, Moonta, Wallaroo, Port Victoria, Warooka, Port Broughton, Port Wakefield.
West area:	Port Lincoln, Cowell, Port Neil, Coffin Bay, Tumby Bay, Port Kenny, Streaky Bay, Thevenard, Ceduna.

Appendix II

Table 21

ANNUAL CATCH BY AREAS FOR TASMANIA

(Weight in 1000 lb)

Year	Areas								Total	Victoria	Grand Total
	1	2	3	4	5	6	7	8			
1942	85	24	—	1	15	72	226	1	424	31	455
1943	62	29	2	8	10	52	289	47	499	51	550
1944	35	94	4	100	14	11	238	61	557	89	646
1945	53	64	34	196	27	13	147	71	605	69	674
1946	130	51	3	221	43	7	151	48	654	127	781
1947	168	86	5	308	80	37	293	28	1005	568	1573
1948	330	21	2	113	146	40	385	118	1155	1015	2170
1949	180	36	34	104	161	17	256	53	841	868	1709
1950	107	15	16	37	153	3	384	11	726	1147	1873
1951	78	39	14	3	99	4	252	26	515	1078	1593
1952	82	143	18	27	61	5	293	2	631	1110	1741
1953	78	80	44	39	53	8	287	17	606	1362	1968
1954	61	170	45	15	52	6	261	2	612	1166	1778
1955	5	77	61	14	17	10	213	7	404	845	1249
1956	25	4	27	14	5	2	159	1	237	599	836

THE FAMILY PYRAMIDELLIDAE (MOLLUSCA) FROM NORTHERN AUSTRALIA

By C. F. Laseron*

[*Manuscript received May 5, 1959*]

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Summary

This paper reviews for the first time the family Pyramidellidae from northern Australia. The area includes the Solanderian zoogeographical province, and part of the Dampierian province. All species, whether previously described or now proposed as new, are figured and discussed. The division of the family into three new subfamilies is also proposed. In all 150 species or probable species belonging to 40 genera are reviewed. Of the genera 15 are proposed as new, and of the species 90 are proposed as new, and seven are left specifically unnamed pending the acquisition of more material. A key to the subfamilies and Australian genera is provided.

I. INTRODUCTION

This paper is the first to attempt to review in detail the whole of the family Pyramidellidae from northern Australia, that portion from southern Queensland to Darwin. This area includes the whole of the Solanderian zoogeographical province, and portion of the Dampierian province. The latter is included as the boundaries of the two provinces are as yet imperfectly defined, particularly in relation to the Mollusca. Moreover, so little collecting of small Mollusca has been done in the area west of the Torres Strait that any information, however limited, is a direct contribution to our knowledge of the marine fauna.

In all approximately 150 species belonging to 40 genera are here discussed and figured. The number of species is approximate, as several, though figured for future reference, have been left unnamed pending the acquisition of more and better material. Even so the list of species is probably far from complete, though it is believed most of what might be called the common and typical forms have been covered. Some others have been seen, of which the material is too poor or fragmentary to describe, and these have been left for future workers on the group. Of the species 90 are now proposed as new, and of the genera 15.

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*Deceased June 27, 1959.

The family as a whole is a very large one, with a multitude of species, mostly small or minute, ranging from a little over 1 mm to 10 mm, with a few larger forms up to 30 or 40 mm in length. The range is world-wide, with probably the densest concentration in the Indo-Pacific regions. The origin was probably in the Cretaceous, for by the early Tertiary the family was well developed, and numerous fossils found in many countries are closely related to living forms.

Previous Work.—A few of the larger, tropical species were described by various authors in the early nineteenth century, but the first extensive work on the smaller species was done by A. Adams. In 1854, in Sowerby's "Thesaurus Conchyliorum", he published a monograph on the family, and in various papers from 1860 to 1867 described many additional species and some genera, mainly from China and Japan. Little further work was done in the Pacific during the remainder of the century, except for the description of odd species by Pease and other authors.

The next comprehensive work was by Dall and Bartsch (1904) who published a suggested classification of the whole family, supplementing it (1909) with an extensive monograph on the western American species. These works were a valuable contribution to a knowledge of the family, and a considerable advance on anything done before, but unfortunately contained a number of contradictions and errors, particularly in the designation of type species for the various subgenera used. Some of these errors have been perpetuated by subsequent authors without apparent checking, and have caused considerable confusion. Nevertheless the 1909 paper was the first to monograph the family from a particular geographical area, illustrating and describing all species, including those described or illustrated before, and thus forming a foundation on which others could build.

In the south-western Pacific work was for many years confined to the description of individual species from various localities, under a few generalized generic names which had long been in use. Brazier (1877) described a number of species from northern Queensland, and Watson (1886) described others collected by the *Challenger* Expedition, mainly from the Torres Straits. Hedley, in various papers from 1902 to 1909, also described a number of species, mainly from various localities on the Great Barrier Reef, as well as others from the Peronian Province in New South Wales.

The next comprehensive work on lines initiated by Dall and Bartsch was by Laws in eight papers from 1937 to 1941. In these he reviewed the whole of the New Zealand species, both Recent and Tertiary, and for the first time attempted the correlation of living with fossil forms.

Extending the work to the Australian continent, Laseron (1951) reviewed, figured, and described all the species from the New South Wales coast, which virtually coincides with the Peronian zoogeographical province. The present paper is a continuation, covering the species of the Solanderian province, i.e. the coast of Queensland including the Great Barrier Reef, and also the Dampierian province, i.e. the northern Australian coast from the Torres Straits to Darwin. The latter portion is not here separated from the Solanderian because the results must be far from complete, for very little collecting has been done, and only limited material is available from this area.

With the completion of this paper it is hoped that similar studies will be undertaken by others from other areas, from New Caledonia, Fiji, from New Guinea and the adjacent islands, from the Philippines and Japan. Only then can a comprehensive picture be given of the family from the whole of the Pacific Region.

TABLE 1

GEOGRAPHICAL POSITION OF LOCALITIES

Locality	Lat. (S.)	Long. (E.)
North-west Australia		
Darwin	12° 20′	130° 50′
Gulf of Carpentaria		
Rose River	14° 15′	135° 45′
Sweers Island	15° 55′	139° 42′
Torres Straits and New Guinea		
Thursday Island	10° 59′	142° 12′
Prince of Wales Island	10° 40′	142° 12′
Cape York	10° 41′	142° 33′
Albany Passage	10° 39′	142° 35′
Darnley Island	9° 35′	143° 45′
Murray Island	9° 54′	144° 0′
Flinders Passage	10° 38′	142° 18′
Gannet Passage	10° 35′	141° 55′
Port Moresby	9° 25′	147° 8′
Raine Island	11° 33′	143° 59′
Queensland East Coast		
Cape Sidmouth	13° 26′	143° 43′
Princess Charlotte Bay	14° 50′	144° 0′
Cape Flattery	15° 0′	145° 26′
Cairns	16° 54′	145° 44′
Bowen	20° 1′	148° 16′
Keppel Bay	23° 25′	150° 15′
Port Curtis and Gladstone	23° 58′	151° 20′
Hervey Bay	25° 0′	153° 0′
Caloundra	26° 49′	153° 9′
Moreton Bay	27° 0′	153° 15′
Great Barrier Reef		
Hope Islands	15° 45′	145° 30′
Endeavour Reef	15° 50′	145° 40′
Low Isles	16° 23′	145° 35′
Michaelmas Cay	16° 35′	146° 0′
Palm Islands	18° 40′	146° 40′
Lindeman Island	20° 30′	149° 4′
Brampton Island	20° 47′	149° 18′
Capricorn Group*	23° 30′	152° 0′
Lady Elliott Island	24° 7′	152° 46′

*Heron Island, Masthead Island, and North-west Island.

Material for Research.—It is believed that the material for this research is practically all that is at present available from any source. The wealth of large and striking species of Mollusca on the Great Barrier Reef of Queensland has largely blinded collectors to the even greater wealth and variety of small species, and as a result these have been largely neglected. Fortunately the late Charles Hedley, when conchologist to the Australian Museum, and others such as A. McCulloch and Brazier, were alive to their importance, and took every opportunity of adding to the Museum's collections. Though some of this material has deteriorated in glass tubes, it has provided a splendid basis on which to work. In later years Mr. T. Iredale, who succeeded Mr. Hedley as conchologist, was also greatly interested in the small shells, and made extensive collections from Michaelmas Cay, the Low Isles, and other localities. Of the present-day collectors the author has received material from Mr. M. Ward, Mrs. J. Kerslake, Mr. J. Voorwinde, and Mrs. M. Price, but unfortunately one or two collectors would not part with treasured specimens, and perforce reference to them has been omitted. Finally, the best present-day collections have been made by the author's son John Laseron from Darwin, Thursday Island, Port Moresby, from the Capricorn Group, and from Bowen, Port Curtis, and Hervey Bay on the Queensland coast. These have provided much of the best material here described.

Table 1 is a list, with their geographical positions, of all the localities from which material was available for study.

II. Classification and Distribution

(a) *Classification*

The true classification of the Pyramidellidae, as of so many of the families of small molluscs, is still largely unknown. Family characteristics are based on both the animal and the shell, but as the soft parts have been studied in relatively few species, the shell itself is generally the only existing guide to classification. A good review of what is known of the family characteristics was given by Dall and Bartsch (1904, 1909), to which the present paper has very little to add. It follows that, in the absence of knowledge of the anatomy on many groups of species, there are still anomalies, and the inclusion of some groups within the family is open to doubt. For instance *Obtortio*, included by Dall and Bartsch, is considered by other authors to belong either to the Rissoidae or to a separate family altogether. Species of *Obtortio* from northern Australia were indeed reviewed in a recent paper on the Rissoidae of that area.

The only Australian species of which the animal has been described is *Linopyrga pascoei* (Angas). This was by Hedley (1917, p. 716, pl. 46, fig. 5). Hedley suggests from this that the Pyramidellidac should probably be placed in the Ophisthobranchiata near the Acteonidae.

There are several shell characters which can be taken as a guide to the family. The first is the protoconch, which seems invariably anastrophic, though at times, where it is wholly or partially immersed in the summit, its exact nature is hard to determine. The anastrophic protoconch is sinistral in its initial coiling, sometimes helicoid, sometimes planoid, or even almost spherical. The change to dextral coiling may be sudden, so that the sinistral portion is twisted obliquely to the axis of the mature shell; it may lie prostrate on the summit; or it may even be inverted and immersed in the summit. In a few groups the change from sinistral to dextral coiling has a short intermediate stage when the juvenile shell becomes nearly straight. The whole protoconch is then very exsert, with the sinistral portion quite free and oblique, giving a curious and characteristic appearance as in *Koloonella*, hereinafter described.

Another guide to the family is the aperture which is fairly constant throughout. It is entire, without posterior or anterior canals or sinuses, and the peristome is, except in a few anomalous species, incomplete. The inner margin is free and stands up from the preceding whorl; it is either straight or curved; either columnar or more or less reflected; either smooth (as in the Turbonillinae) or more often bearing one to three more or less oblique folds. In those species with one fold this is not always visible from in front, but can be seen only within the aperture or when the shell is broken. Most of the species are imperforate, but a few groups are deeply umbilicate, though the umbilicus is always narrow.

The family is wholly marine, if exception be made of one or two groups such as *Koloonella*, which may possibly extend into estuarine or brackish water. The distribution is world-wide, within and without the tropics, both living and as fossils. If their origin was in the Cretaceous, they had by the early Tertiary certainly multiplied in species and diverged into generic groups very similar to those of the present day. Such genera as *Turbonilla*, *Chemnitzia*, *Pyrgiscilla*, and others of the Turbonillinae as well as some Odostomiinae are clearly recognizable in the Tertiary rocks of New Zealand, southern Australia, and central America. The last to develop were probably those with two or three columella folds, and as most of these are relatively large shells they are not likely to be overlooked as fossils.

(*b*) *Distribution*

How many species of Pyramidellidae exist is not yet known, but the number must be very great. The greatest concentration seems to be in the Pacific, where already many hundreds of species have been described, and where the ultimate total is almost certain to exceed one thousand. The Indian Ocean, where the family has as yet hardly been touched, will probably provide as many more.

Many of the species seem endemic within narrow areas, but others, particularly the larger tropical forms, have a wide range, both north and south of the equator. But between the eastern and western Pacific there is a wide gulf, and as far as is known, not one species is common to the two regions. Very little is known of the life history of the majority of species, but apparently very few have a long, free-swimming larval stage. For this reason very few have been found in any of the true oceanic islands.

In depth the family lives from low tide to the great depths of the ocean. Very few species are found in the intertidal zone, and then only in pools which remain filled during low tide. The greatest number of species is found from extreme low tide to about 20 fm, but the *Challenger* Expedition obtained specimens down to 1400 fm in the Mediterranean, from 1000 fm in the Atlantic and from 500 fm in the Pacific. Many species live in cracks or under rocks or coral boulders on the reefs, but others, including many turbonillids, live exclusively on algae. Specimens dredged from sandy or muddy bottoms are generally dead, and there is no certainty that these are their habitats, but as they often occur in considerable numbers there seems little doubt that they live there. The absence of a radula, which is accepted as one family characteristic, suggests that their feeding is largely siphonal, their food the microscopic life of the sea.

Most of the species discussed in this paper are recorded from more than one locality, sometimes from localities far apart, both from the Barrier Reef and the shores of the mainland. It is curious that though the Solanderian and Dampierian have been recognized as distinct provinces, a number of species from Bowen and Port Curtis on the mid Queensland coast have been recognized also from Darwin, distant over 1200 miles and well within the Dampierian Province. But only one or two species so far are definitely common with the temperate Peronian province in the south, except in the overlap area in the extreme south of Queensland.

(c) *Division into Subfamilies and Genera*

In the early days of conchology when comparatively few species of Mollusca were known, a broad grouping into a few genera was sufficient. As more and more species were discovered new generic names were needed, not only to cover striking new forms, but also to divide groups which were becoming unwieldy. There was not always unanimity how such groups of species should be subdivided. If a genus be defined as a group of related species, there is bound to be a difference of opinion as to the degree of relationship necessary. There is also difference in opinion as to the value of different characters for generic purposes, such for instance as the protoconch, sculpture, form, or aperture. But most modern authors are in agreement that extensive subdivision of the larger families is necessary. Writing of the Pyramidellidae, Dall and Bartsch (1904, p. 1) state: "Where a group is composed of such a multitude of species it seems more convenient in practice and leads more efficiently to clear thinking, to subdivide the groups sufficiently to make it reasonably clear where a given species belongs in the series."

Even then Dall and Bartsch were content to retain only *Pyramidella*, *Odostomia*, *Turbonilla*, and *Murchisonella* as full genera, to which other names, either previously used or newly proposed, were relegated as subgenera, or even as sections of subgenera. In later papers they abandoned sectional names and used only genera and subgenera. Laws, in his papers from 1937 to 1941, partially followed Dall and Bartsch, but used only generic names, grouping them however as turbonillid genera, syrnolid genera, eulimellid genera, etc. Laseron (1951) used only generic names. Whether generic or subgeneric names be used for many groups of species seems immaterial, but the objection to subgeneric names is that they are often unwieldy, and they assert relationship which is doubtful, thus leading to false conclusions in the fields of ecology and distribution.

It is now proposed to raise the status of the genera used by Dall and Bartsch to the status of subfamilies, for which the names Pyramidellinae, Odostomiinae, and Turbonillinae are suggested, *Murchisonella*, of which the author has no knowledge, being left in abeyance. This should greatly simplify the nomenclature of the whole family. The primary difference between the three subfamilies is that the Pyramidellinae have two or three columella folds, the Odostomiinae have one, and the Turbonillinae have none.

Of the validity of many of the genera here used there will still be a difference of opinion, caused sometimes by a curious prejudice based largely on the size of the shell. If such minute shells as *Hinemoa*, *Herviera*, and *Miralda* were an inch or upwards in size, their characters would be so distinctive that none would doubt their full generic status, nor would the validity be challenged of certain other groups of slightly larger shells such as *Cingulina*, *Koloonella*, *Zonella*, and others. On the other hand *Turbonilla* and *Chemnitzia* are separated only by the axial ribs continuing to the base on the former and terminating on the periphery on the latter. It might be held that this character is of doubtful generic or even subgeneric value. Here, however, the group of species is very large, the character is remarkably clear-cut, and affords a ready and practical method of subdivision.

The characters used for generic determination are mainly form and sculpture. There is, for instance, a sharp line of demarcation between groups of species which are quite smooth, others with sculpture of axial ribs only, and those with spiral sculpture only. Others again have both axial and spiral sculpture combined in various ways. The form varies, and distinction can be made between groups in which the shells are elongate, acuminate, and many-whorled, and those which are broader, ovate in contour, and with comparatively few whorls. This distinction is not, however, as clearly defined as the sculpture, and is considered as additional rather than of primary generic importance. The same differences in form and sculpture repeat themselves in the three subfamilies.

The protoconch has not been found of great use in generic separation, though Laws used it in New Zealand for this purpose. The differences mentioned by Laws seem rather obscure, particularly where the protoconch is partially or wholly immersed in the summit, and they are hard to follow. In some groups, however, the protoconchs follow the general generic pattern, for instance in *Koloonella*, where they are well exsert and curiously twisted, or in *Turbonilla* and *Chemnitzia*, where they are helicoid and prostrate on the summit. The protoconch then becomes one of other generic characters. In the subfamily Pyramidellinae, though the shells are often relatively large, the protoconch is generally very minute.

III. Key to Subfamilies and Genera

Key to Subfamilies

1.	With 2–3 columella folds	Pyramidellinae
	With 1 columella fold	Odostomiinae
	Without columella fold	Turbonillinae

Key to Australian Genera

Subfamily Pyramidellinae

1.	With 3 columella folds	2
	With 2 columella folds	7
2(1).	Shells large to medium, ovate, large body whorls	3
	Shell elongate, many short whorls	5

3(2).	Umbilicate	*Pyramidella* Lamarck
	Not umbilicate	4
4(3).	Smooth	*Milda* Dall & Bartsch
	Axial sculpture only	*Aphalista*, gen. nov.
	Axial and spiral sculpture	*Otopleura* Fischer
5(2).	Umbilicate	*Urambella*, gen. nov.
	Not umbilicate	6
6(5).	With peripheral groove	*Wingenella*, gen. nov.
	Without peripheral groove	*Voluspa* Dall & Bartsch
7(1).	Without sculpture	8
	With sculpture	*Tropaeas* Dall & Bartsch
8(7).	Umbilicate	*Tiberia* Monterosato
	Not umbilicate	*Cossmannica* Dall & Bartsch

Subfamily Odostomiinae

1.	Without sculpture	2
	With sculpture	5
2(1).	Elongate, acuminate, many short whorls	3
	Short, few whorls	4
3(2).	Sutures plain	*Syrnola* A. Adams
	Sutures channelled	*Colsyrnola* Iredale
4(2).	Sutures plain	*Odostomia* Fleming
	Sutures channelled	*Parodostomia*, gen. nov.
5(1).	Spiral sculpture only	6
	Axial sculpture only	7
	Axial and spiral sculpture	11
6(5).	Sculpture of strong spiral ribs	*Hinemoa* Oliver
	Sculpture fine, incised spiral lines	*Evalea* A. Adams
7(5).	Whorls sinuate, sculpture fine and oblique	*Kunopia*, gen. nov.
	Whorls not sinuate, ribs straight and strong	8
8(7).	Peristome complete	*Herviera* Melvill
	Peristome not complete	9
9(8).	With peripheral sulcus	*Tathrella*, gen. nov.
	Without peripheral sulcus	10
10(9).	Whorls rounded	*Elodiamea* de Folin
	Whorls medially indented	*Exesilla*, gen. nov.
11(5).	Base excavate	12
	Base rounded	13
12(11).	Single spiral rib, sutures not deeply grooved	*Paregila* Laseron
	Double spiral rib, sutures deeply grooved	*Babella* Dall & Bartsch
13(11).	Whorls angled	14
	Whorls not angled	15
14(13).	Whorls angled above sutures	*Egila* Dall & Bartsch
	Whorls angled below sutures	*Eurathea*, gen. nov.
15(13).	Axial ribs on upper part of whorls only	*Miralda* A. Adams
	Axial ribs persistent to base	16
16(15).	Spiral sculpture overrides axial ribs	*Quirella*, gen. nov.
	Spiral sculpture in intercostal spaces only	17
17(16).	Spiral sculpture fine threads	*Linopyrga* Laws
	Spiral sculpture incised lines	*Pyrgulina* A. Adams

Subfamily Turbonillinae

1.	With sculpture	2
	Without sculpture	8
2(1).	Spiral sculpture only	*Cingulina* A. Adams
	Axial sculpture only	3
	Axial and spiral sculpture	4
3(2).	Axial ribs persistent to base	*Turbonilla* Risso
	Axial ribs stop at periphery	*Chemnitzia* d'Orbigny
4(2).	Spiral sculpture as fine threads or incised lines	5
	Spiral sculpture as strong ribs	7
5(4).	Spiral sculpture overrides axial ribs	*Mormulasta*, gen. nov.
	Spiral sculpture in intercostal spaces only	6
6(5).	Axial ribs continuous to base	*Pyrgiscus* Philippi
	Axial ribs stop at periphery	*Pyrgiscilla* Laws
7(4).	Spiral rib below suture broken into tubercles	*Zaphella*, gen. nov.
	Spiral rib on periphery	*Amamimormula* Kuroda
8(1).	Umbilicate	*Myxa* Hedley
	Not umbilicate	9
9(8).	Whorls not angulated	10
	Whorls angulated	11
10(9).	Thin and transparent, margin of aperture straight	*Koloonella*, gen. nov.
	Solid, aperture rissoid, outer margin sinuate	*Paradoxella*, gen. nov.
11(9).	Spiral rib at suture	*Zonella*, gen. nov.
	Without spiral rib at suture	*Instarella*, gen. nov.

IV. Description of Species

Unless otherwise stated, all types, paratypes, and specimens illustrated or referred to, if not already in the Australian Museum, Sydney, are now presented to that institution.

Subfamily **PYRAMIDELLINAE**

Genus MILDA Dall & Bartsch

Type species *Pyramidella ventricosa* Quoy & Gaimard = Guerin.
Milda Dall & Bartsch, 1904, p. 4.

The generic description given is: "columella folds 3, shell umbilicated, basal fasciole present, surface less polished than in *Pyramidella*".

This would be a satisfactory description except that the type species chosen is not umbilicate. As the type is the final criterion the term "umbilicate" must be omitted as a generic characteristic. The term basal fasciole is obscure, but evidently refers to a character occurring in a number of species with 3 columella folds. The posterior fold, which is the most prominent, extends across the base, and as a rounded rib spirally encircles the umbilical area to the anterior extremity. The column of the inner margin of the aperture bearing the two lesser folds is separated within this. This character evidently develops only after full maturity, and specimens not so mature do not show it.

In order to distinguish *Milda* from *Voluspa* Dall & Bartsch, and apart from the deletion of the character umbilicate, it is necessary to add to the generic description by stating that *Milda* includes large shells of generally broad ovate shape, with large body whorls and comparatively short spires.

MILDA VENTRICOSA (Guerin)

Fig. 1

Pyramidella ventricosa Guerin, 1831, p.2.
Pyramidella ventricosa Quoy & Gaimard, 1832, pl. 65, figs. 3, 7.

The type locality is Vanikoro, Santa Cruz, and the species is distinctive and well distributed in the western Pacific. The colour pattern of irregular brown patches is generally a good recognition character, but it varies considerably, some individual specimens having a few isolated patches, while in others the patches are confluent and cover much of the surface. Occasionally it may be pure white. The specimen here figured is from Bowen (J. Laseron) and is 26 mm in length. Other specimens examined are from Lindeman Island (T. Iredale) and Cape York (Mrs. J. Kerslake).

When Dall and Bartsch made this the type of their subgenus *Milda* they referred to it as umbilicate, but neither in the original description nor figure, nor in the many specimens examined, is there any trace of umbilication.

MILDA CINCTA (Reeve)

Figs. 2 and 3

Pyramidella cincta Reeve, 1842, p. 149, pl. 207, figs. 2 and 4.

This is another widespread species in the western Pacific, easily recognizable by the broad brown spiral band surrounding the whorls. No locality was given for the type. The specimen figured (Fig. 2) is from Edgecumbe Bay, Queensland, and is 27 mm in length. Material has also been examined from Michaelmas Cay (T. Iredale), Green Island, Cairns (Mrs. May Price), and other localities.

A feature of the species is a strong tuberculation within the outer lip of the aperture. This tuberculation seems to be either intermittent or occurs only in the early stages of growth, as in many adult shells it is either invisible or is only visible deep within the aperture. A number of smaller specimens were at first thought to be entirely different, but it has been concluded that they are probably juveniles of *cincta*. One from Murray Island, 5 mm in length, is here figured (Fig. 3).

Genus APHALISTA, gen. nov.

Type species *Pyramidella mitralis* A. Adams.

Ovate to cylindrical shells with large body whorls, sculpture of strong rounded axial ribs without any spiral threads or cords, not umbilicate, columella folds 3 with a basal fasciole similar to that of *Milda*. The form and aperture generally are like *Milda* but the strong axial ribs at once distinguish it. It is curious that Dall and Bartsch, with their emphasis on sculpture, should have overlooked in their grouping this very distinctive form.

APHALISTA MITRALIS (A. Adams)

Figs. 4–6

Pyramidella mitralis A. Adams, 1854, p. 814, pl. 52, fig. 9.

The type locality is the Philippine Islands. The form and size are very variable, ranging from individuals which are relatively large and ovate to those which are little more than half the size and nearly cylindrical in shape. The colour is white to cream with irregular brown patches. Two specimens, both from Michaelmas Cay (T. Iredale) are here figured and show about the extremes in variability. The larger (Fig. 4) is 17 mm in length, the smaller (Fig. 6) 9 mm. Series from Michaelmas Cay and Murray Island (C. Hedley) both show this variability, and every gradation is found between the two extremes. Specimens have also been examined from Low Isles (T. Iredale) and other localities. To supplement the original description the following details may now be added. Protoconch nearly spherical, minute, on the acute summit, followed by 2 small smooth dextral whorls. Total whorls 9, short, slightly rounded, and restricted at the sutures, body whorl large, about half the total length. Sculpture of large, rounded axial ribs, less than their own width apart, about 24 to the whorl, continuous from the suture to the base, spiral sculpture absent. Aperture semicircular, with a wide band of callus internally on the body whorl, outer and anterior margins rounded, the latter anteriorly angled. Inner margin expanded behind into a rounded plate, bordered by a rib formed by a continuation of the main posterior fold which is nearly transverse. Below this on the columnar inner margin are 2 smaller folds.

Genus OTOPLEURA Fischer

Type species *Voluta auriscati* Dillwyn.
Otopleura Fischer, 1885, p. 787.

Large, broadly ovate shells, the body whorl long, spire comparatively short, sculpture of strong, axial ribs, with spiral cords crossing the intercostal grooves, not umbilicate. Aperture with 3 columella folds and basal fasciole as in *Milda*.

Both Fischer and Dall and Bartsch quote the type as *Voluta auriscati* Chemnitz, but as Chemnitzian names are now generally discarded as not being binomial, Dillwyn's (1817) use of the name becomes the first legitimate reference.

OTOPLEURA AURISCATI (Dillwyn)

Figs. 7 and 8

Voluta auriscati Dillwyn, 1817, p. 503.

The type locality is Vanikoro, Santa Cruz. It is common and widely distributed in the western Pacific, and is a striking and distinctive species with its turreted whorls, beading just below the sutures, and its cream and brown variegated colouring. It occurs in a number of localities on the Great Barrier Reef and on the Queensland coast. The specimen figured is one of a series collected by J. Laseron from Port Curtis. Its length is 20 mm.

OTOPLEURA AUSTRALIS, sp. nov.

Fig. 9

Shell large, narrowly ovate and elongate, colour cream with irregular brown patches. Protoconch missing in the holotype. Remaining whorls 10, short, flattened, narrowly stepped above, slightly bent in below with a narrow keel to the sutures, body whorl large but relatively shorter than in *O. auriscati*, rounded at the base. Sculpture of raised, rounded axial ribs, less than their own width apart, about 30 to the whorl, persistent to the base. Spiral sculpture of strong, close cords which cross the intercostal spaces but do not override the axial ribs. Aperture triangular, with a wide band of callus within on the adjoining whorl, making the peristome complete, outer margin flattened and slightly inbent, anterior margin flattened and angled with the inner margin, inner margin a curved column with 3 transverse folds, the posterior the largest, and continuous, forming a small rib encircling the umbilical area. Length 24 mm.

Locality.—North-west Island, Capricorn Group; holotype.

Remarks.—This unique species can readily be distinguished from *O. auriscati* by the form, less turreted whorls, shorter body whorl, more numerous axial ribs, and by the absence of the beading immediately below the sutures.

Genus URAMBELLA, gen. nov.

Type species *Urambella ballerina*, sp. nov.

Elongated acuminate shells with numerous short whorls, smooth polished surfaces and no sculpture, except occasionally a few weak axial puckers near the top of the whorls, the spire perforated by a narrow umbilicus, inner margin columnar with 3 folds, the posterior the largest.

In form, aperture, and lack of sculpture, this is very similar to *Voluspa* Dall & Bartsch, but the critical character separating it is the narrow and deep umbilicus.

URAMBELLA BALLERINA, sp. nov.

Figs. 10 and 11

Shell medium to large, thin, conical, and elongate, apex acuminate, colour white with thin spiral brown bands, 2 on the earlier whorls, 3 on the body whorl. Protoconch minute, anastrophic, prostrate on the summit. Mature whorls 10, short, increasing regularly, slightly rounded, narrowly channelled at the sutures. Sculpture none, surface smooth and polished. Base with a narrow but deep umbilicus, perforating the spire, but partly hidden by the reflection of the inner margin of the aperture. Aperture semicircular, extended anteriorly, outer and anterior margins thin and rounded, inner margin straight, columnar, and reflected, with 3 folds, the posterior the largest, continuous across the column and flanking it to the anterior extremity. Length 22 mm.

Localities.—Green Island, Cairns (Mrs. M. Price), holotype; Michaelmas Cay (T. Iredale).

Remarks.—This species, the type of the genus, is well marked and distinctive, the form and colour being good recognition characters.

URAMBELLA AFFINIS, sp. nov.

Fig. 12

Shell of medium size, narrowly conical, elongate, and acuminate, colour cream, holotype with a narrow spiral brown band on the periphery of the body whorl and another on the base, other specimens with an additional brown band below the sutures. Protoconch minute, anastrophic, prostrate on the summit. Mature whorls 10, short, nearly flat, channelled at the sutures. Defined sculpture none, the surface generally smooth and polished, but faint growth lines in some specimens are exaggerated to slight axial puckers below the sutures. Base with a narrow, deep, circular umbilicus. Aperture semicircular, outer and anterior margins thin and rounded, inner margin curved and columnar, reflected to partially obscure the umbilicus, folds 3, the posterior the strongest, the other 2 weak and oblique. Length 14 mm.

Localities.—Darnley Island (C. Hedley), holotype and two paratypes; 4–14 fm Albany Passage (C. Hedley).

Remarks.—Compared with *U. ballerina* this species is smaller and relatively narrower, the whorls are flatter and the sutures more deeply channelled. It is the species which has been recorded from Queensland as *Obeliscus terebelloides* A. Adams (1854, p. 808, pl. 171, fig. 18) which was described from an unknown locality. It is certainly close to Adams's figure and description, but the sutures are more deeply channelled, and Adams states that the columella folds number only two.

URAMBELLA PLICATA, sp. nov.

Fig. 13

Shell large, broadly conical, elongate, apex acuminate, thin, colour white with thin brown spiral bands, 4 on the body whorl, one just above the suture on the earlier whorls. Protoconch missing on the holotype, but from the acuminate apex it must be minute. Mature whorls 9, short, very slightly rounded, slightly restricted but not channelled at the sutures. Sculpture none except a few faint growth lines, the surface smooth and shining. Umbilicus narrow, round, and deep, partially obscured by the reflection of the inner margin of the aperture. Aperture semicircular, well extended anteriorly, outer margin thin and rounded, with about 6 strong plications within, anterior margin rounded, inner margin columnar and widely reflected, the reflection becoming semitubular as an extension of the umbilicus, folds 3, extending obliquely right across the column, the uppermost the largest. Length 18 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype; Port Curtis (T. Iredale).

The Port Curtis specimen, though faded, matches the holotype in all details, and has the same strong plications within the aperture. This species resembles *U. ballerina*, but is relatively much broader, and in no specimens of either *ballerina* or *affinis* has any trace been observed of plications within the aperture.

Genus WINGENELLA, gen. nov.

Type species *Wingenella eburnea*, sp. nov.

Elongate, acuminate shells of conical form, with many short whorls, the whorls generally flat, with no sculpture and polished surfaces, a spiral groove on the periphery, no umbilicus, the columella folds 3.

It was at first proposed to follow Dall and Bartsch in using *Longchaeus* Morch for a large group of Pacific shells with the above characters, but the confusion surrounding *Longchaeus* is so great that it can best be cleared by the proposal of a new genus. When Morch proposed *Longchaeus* (1875, p. 158) he did not designate a type and gave the brief description "T. imperforata, ult. sulco media". It will be noticed that apart from being imperforate the only generic character is that the last whorl has a peripheral groove. The name might well be rejected as nomen nudum, though Morch listed as examples *Obeliscus punctatus* Chemnitz and two other species, and followed with a description of *Obeliscus* (*Longchaeus*) *candida* Meusch from St. Thomas in the West Indies. Dall and Bartsch (1904, p. 4) selected *punctatus* as the type. This was doubly unfortunate, as *punctatus* has no status, Chemnitzian names having been rejected as not binomial, though the same species was later described by Lamarck as *Pyramidella maculosus*. Furthermore this species has no groove on the periphery of the body whorl. If *Longchaeus* be retained, the species *candida* would be a better type. However, as this has but two columella folds, it will not fit with Dall's and Bartsch's use of the genus, nor with any of the Australian species here discussed.

WINGENELLA EBURNEA, sp. nov.

Figs. 14–16

Shell large, conical, elongate, and acuminate, imperforate, colour ivory to horn, with a few irregular brown patches. Protoconch minute, almost spherical, half immersed in the summit. Mature whorls about 20, short, nearly flat, sutures channelled. Sculpture none except faint growth lines, surface polished, a narrow spiral groove on the periphery of the body whorl. Aperture not extended anteriorly, semicircular, outer and anterior margins thin and rounded, inner margin columnar with 3 folds, the posterior continuous and spirally encircling the umbilical area, the anterior 2 folds small. Length of holotype 36 mm.

Localities.—North-west Island, Capricorn Group, holotype and a number of paratypes; Lindeman Island (T. Iredale).

Remarks.—The form is similar to *Voluspa maculosa* (Lamarck), but the peripheral groove separates it both specifically and generically. Figure 16 is a horn-coloured specimen from Lindeman Island, 21 mm in length, which has a slightly different appearance, but it may not be mature, being smaller and having fewer whorls than the type. It is here figured for comparison.

WINGENELLA PRICENA, sp. nov.

Figs. 17 and 18

Shell large, conical, elongate, narrow, and acuminate; colour generally white, but occasionally pale brown. Protoconch minute, anastrophic, prostrate on summit.

Mature whorls about 16, short, nearly flat, sutures narrowly channelled. Sculpture absent, except for faint growth lines, the surface smooth and shining, a very narrow spiral groove on the periphery of the body whorl. Aperture extended anteriorly, semicircular, the outer and anterior margins thin and rounded, inner margin a wide plate, folds 3, the posterior large, continuing across the inner margin and bordering it as a rib to the anterior extremity, the two anterior folds small and oblique. Length 28 mm.

Localities.—Green Island, Cairns (Mrs. M. Price), holotype (Fig. 17) and one paratype; Curtis Island, Port Curtis (J. Laseron); Michaelmas Cay (T. Iredale); Lindeman Island (T. Iredale); Rose River, Arnhem Land (Mrs. J. Kerslake).

Remarks.—In general characters this species is very close to *W. eburnea*, but is uniformly narrower, and the aperture is more extended anteriorly. A single, even larger, imperfect specimen, brown in colour, from Lindeman Island, is even narrower than the holotype, and is doubtfully assigned to this species. It is 31 mm in length, and is here figured for comparison. The species is named after Mrs. M. Price of Cairns, who kindly made material from her collection available.

WINGENELLA OBTUSA, sp. nov.

Fig. 19

Shell small for the genus, conical, elongate, with a blunt apex, colour yellow. Protoconch small, entirely immersed in the blunt apex. Mature whorls 8, short, nearly flat, sutures deeply channelled. Sculpture absent, the surface smooth and polished, body whorl with a deep, relatively wide, spiral peripheral groove. Aperture well extended anteriorly, semicircular, outer margin nearly flat, anterior margin rounded, inner margin columnar, with a strong posterior transverse fold and two smaller oblique folds, a small rib encircling the umbilical area. Length 6·5 mm.

Localities.—Caloundra (J. Laseron), holotype and three paratypes; Curtis Island (J. Laseron).

Remarks.—This is smaller than the two preceding species, even though the holotype may not be quite mature, but it is easily distinguished by the blunt apex, colour, and the deeper and wider peripheral groove.

Genus VOLUSPA Dall & Bartsch

Type species *Pyramidella auricoma* Dall.
Voluspa Dall & Bartsch, 1904, p. 4.

A full generic description was not published, but a study of the key shows that the shell is not umbilicate, the columella folds are 3, the surface is smooth and polished, and the periphery of the body whorl is not sulcate. To this can be added from the type that the shell is long, conical, and acuminate, and that the whorls are many and short.

VOLUSPA MACULOSA (Lamarck)

Fig. 20

Pyramidella maculosa Lamarck, 1816, p. 11, pl. 452, figs. 1*a*, 1*b*.
Pyramidella punctata Schubert & Wagner ex Chemnitz, 1829, p. 152, pl. 239, figs. 4099*a*, 4099*b*.

This the largest and possibly the most widespread species of the family in the western Pacific. The specimen here figured is from Darnley Island (M. Muller) and is so close to the original figure that it might well have been drawn from the individual specimen. It is 40 mm in length. The regular brown spotting makes it a conspicuous and easily recognized species.

Reference has already been made to the confusion surrounding the genus *Longchaeus* Morch, and reasons given for rejecting this species as its type. Examination of series from Low Isles (T. Iredale), Green Island, Cairns (Mrs. M. Price), Murray Island, and other localities, do not show any trace of a peripheral groove, and it comes clearly within *Voluspa* as interpreted by its authors.

Genus TIBERIA Monterosato

Type species *Pyramidella minuscula* Monterosato.
Tiberia Monterosato, 1875, p. 5.

Tiberia was proposed for smooth, ovate shells with 2 columella folds and a deep umbilicus.

Monterosato clearly indicated the type species which he had previously described from Sicily, where it had before been wrongly identified as *Pyramidella nitidula* A. Adams, the type of which came from Japan. *P. minuscula* is clearly a good species, for it is markedly umbilicate, whereas *nitidula*, from both description and figure, has no umbilicus. Dall and Bartsch (1904, p. 5) erroneously cited *nitidula* as the type of *Tiberia*, an unfortunate carelessness, for while they recognized the umbilicus as an essential character of *Tiberia*, they later (1909) assigned a number of west American species which are not umbilicate to *Tiberia*. It is left for American conchologists to transfer these species to another genus or genera.

TIBERIA QUEENSLANDICA, sp. nov.

Fig. 21

Shell of medium size, solid, broadly conical with a blunt apex, colour white. Protoconch minute, immersed in the dome-shaped summit. Mature whorls 7, short, nearly flat, sutures narrowly channelled, body whorl relatively large, base with a well-defined, moderately wide, round umbilicus, penetrating the whole spire. Sculpture none, the surface smooth. Aperture slightly extended anteriorly, semicircular, outer and anterior margins rounded, inner margin straight and columnar, reflected, the posterior fold strong, the anterior fold weak and oblique, barely visible from in front. Length 5 mm.

Locality.—Thursday Island, holotype and eight paratypes.

Remarks.—The deep umbilicus and two columella folds separate this from other northern Australian species. In form it is like *Pyramidella nitidula* A. Adams (1860) from Japan, but as already stated that species is not umbilicate, and so cannot be considered.

It is actually nearer the shell which Hedley and Petterd identified as *Tiberia nitidula* (A. Adams) from 300 fm off Sydney (1906, p. 216, pl. 38, fig. 13), but has flatter whorls and differs in form. That shell is certainly not *nitidula*, being also deeply umbilicate, and thus needs another name.

Genus COSSMANNICA Dall & Bartsch

Type species *Pyramidella clandestina* Deshayes.
Cossmannica Dall & Bartsch, 1904, p. 6.

Generic characters taken from the authors' key are: aperture suboval, basal fasciole absent, columella folds 2, surface smooth and polished with very faint growth lines, shell not umbilicated.

A few Australian species come within the above generic description and are tentatively placed here, though further investigation may show that some revision is necessary. Amongst genera available for the reception of smooth species with 2 columella folds *Tiberia* is definitely umbilicate, and *Vagna* Dall & Bartsch has, according to the authors, a basal fasciole. *Eulimella* Forbes, though included by Dall and Bartsch in this section as having 2 columella folds, is wrongly placed, as it has no columella fold at all. If *Cossmannica* be applied strictly according to its original description, then it covers a large group in the Pacific Ocean, including many which were referred by Dall and Bartsch to *Tiberia* in their 1909 paper.

Cossmannica jacksonensis (Dall & Bartsch)

Fig. 22

Pyramidella (*Tiberia*) *pusilla jacksonensis* Dall & Bartsch. 1906, p. 325, pl. 26, fig. 8.

This species was based on two specimens from the Paetel collection in Berlin, labelled from Port Jackson in New South Wales. It is doubtful if this locality is correct, as intense collecting in Port Jackson by the present author and many others over the intervening years has failed to rediscover it. Specimens from Thursday Island are, however, very close to the figure and description of the type, and slight differences are well within the limits of individual variation. The specimen figured is 4·7 mm long. The following is a description.

Shell small, solid, narrowly ovate with a convex spire, colour white. Protoconch nearly spherical, half immersed in summit. Mature whorls 6, very slightly rounded, slightly restricted at the sutures, base of body whorl rounded without an umbilicus. Sculpture none, the surface smooth. Aperture extended and narrowed anteriorly, outer margin rounded, with 5 prominent, elongated tubercles within, inner margin columnar, the posterior fold large and prominent, the anterior fold slight and oblique.

Of the various species with two columella folds, this is the only one so far observed with tubercles within the outer margin of the aperture.

Cossmannica exesa, sp. nov.

Fig. 23

Shell of medium size, conical, elongate, with a slightly concave spire, swollen at the base, colour white. Protoconch small, nearly spherical, occupying about half the summit. Mature whorls 8, short, very slightly curved, the sutures narrowly and shallowly channelled, body whorl slightly angled at periphery, base rounded, without an umbilicus. Sculpture none, the surface smooth and polished. Aperture extended anteriorly, outer and anterior margins rounded, inner margin short, straight, columnar, widely reflected, folds 2, prominent and nearly equal. Length 5 mm.

Locality.—5–8 fm Murray Island (C. Hedley), holotype and 12 paratypes.

Remarks.—The slightly concave spire and swollen base give this species quite a distinct facies, making it easily distinguishable from the other species here discussed.

COSSMANNICA SUBCARINA, sp. nov.

Figs. 24–26

Shell of medium size, solid, conical, with a slightly convex spire, white. Protoconch anastrophic, planoidly coiled, nearly spherical, tilted on summit. Mature whorls 6 on holotype, 7 on some other specimens, nearly flat, short, sutures channelled, body whorl slightly angled at periphery. Sculpture none, the surface smooth and shining. Aperture well extended anteriorly, outer and anterior margins rounded, inner margin columnar, widely reflected, with 2 prominent nearly transverse folds, the posterior slightly the larger. Length 4·5 mm.

Localities.—5–8 fm Murray Island (C. Hedley), holotype (Fig. 24) and numerous paratypes; 4–14 fm, Albany Passage (C. Hedley); Bowen (J. Laseron, Fig. 26); Curtis Island, Port Curtis (J. Laseron); Peel Island, Moreton Bay (Mrs. J. Kerslake).

Remarks.—This is a common and widely distributed species on the Queensland coast. It is constant in its characters, except that specimens from the more southern localities are generally a little larger, and with one or two more whorls. The specimen figured from Bowen for comparison is 6 mm in length. It is close to *Pyramidella nitidula* A. Adams from Japan, but can be distinguished mainly by the slight but distinct angulation of the whorls.

Genus TROPAEAS Dall & Bartsch

Type species *Pyramidella subulata* A. Adams.
Elusa A. Adams, 1861, p. 297, (monotype *E. teres* A. Adams), non *Elusa* Walker, 1858.
Tropaeas Dall & Bartsch, 1904, p. 5.

Dall and Bartsch rejected *Elusa* as preoccupied, and proposed *Tropaeas* as a new subgenus with a different type species. The type is a distinctive species, having curious discrepant sculpture, the early whorls following the anastrophic protoconch, being subulate and smooth, while the later whorls are conical, with strong axial ribs and spiral grooves in the intercostal spaces. The columella folds are 2, and it is also umbilicate.

The Australian species here assigned to *Tropaeas* has all the characters of the type species except that it is not umbilicate. If further species are discovered it may be necessary to divide the genus into two, those with and those without an umbilicus.

TROPAEAS IMPERFORATA, sp. nov.

Figs. 27–30

Shell of medium size, elongate, solid, conical, subulate towards the summit, white. Protoconch anastrophic, planoidly coiled, nearly spherical, tilted on the summit. Mature whorls 14, including the smooth whorls towards the apex. The whorls are in two series, the early whorls after the sinistral nucleus varying from 3–5, slightly rounded and restricted at the sutures, smooth, forming a nearly cylindrical, subulate, slender apex. Thence the spire is conical, the whorls short, slightly rounded and restricted at the sutures, and sculptured. The sculpture consists of short, broad, rounded axial ribs, very close together, about 20 to the whorl, ceasing at the periphery, the base of the body whorl rounded and smooth, with no trace of an umbilicus. Spiral sculpture of a few deep grooves crossing the intercostal spaces, 1–2 on the earlier whorls, 2 on the body whorl. Aperture small, extended anteriorly, outer and anterior margins rounded, inner margin straight and columnar, widely reflected, with 2 strong transverse folds, the posterior the larger. Length 14 mm.

Localities.—20 fm off Darnley Island (J. Brazier), holotype (Figs. 27 and 28); Bowen (J. Laseron), juvenile (Figs. 29 and 30).

Remarks.—The holotype is the original specimen recorded and figured by Hedley (1900, p. 504, pl. 25, figs. 19–21) as *Elusa subulata* A. Adams. *Pyramidella subulata* was first described by Adams (1855, p. 177, pl. 20, fig. 6). This species is certainly very close to *subulata* both in form, subulate early smooth whorls, and the later sculpture, but differs by the absence of an umbilicus. From the other characters it is, however, taken to be congeneric. The specimen from Bowen is juvenile and shows 2 more whorls in the subulate apex, but otherwise is apparently the same species. Whether the smooth earlier whorls are part of the mature shell or of the protoconch is of considerable doubt.

Subfamily **ODOSTOMIINAE**

Genus COLSYRNOLA Iredale

Type species *Colsyrnola sericea* Iredale.
Colsyrnola Iredale, 1929, p. 348.

Apart from the specific description of the type, no generic characters were specified, but the shell is like *Syrnola*, elongated with many whorls, and the whorls are shorter, flatter, and the sutures are marked by a deep, V-shaped channel. The inner margin of the aperture also forms a straight column with a single, prominent, transverse fold. This last character indeed suggests the subfamily Pyramidellinae rather than the Odostominae, and except for the single fold, the genus has more in common with *Voluspa* than any other.

Colsyrnola sericea Iredale

Figs. 31 and 32

Colsyrnola sericea Iredale, 1929, p. 348, pl. 38, fig. 16.

The type came from deep-seated dredgings well below the present harbour bed in Port Jackson, New South Wales, where many tropical shells were found, some of them now apparently extinct in New South Wales waters. The length of the type is 26 mm, which is larger than living shells from north Queensland. The specimen here figured is from Lindeman Island (T. Iredale). It is 13 mm long, and except for size, conforms in every detail with the type. The uniform glossy, yellow-brown colour makes it easily recognized.

COLSYRNOLA TRANSLUCIDA, sp. nov.

Fig. 33

Shell of medium size, elongate, regularly conical with an acute apex, colourless, vitreous, and translucent. Protoconch anastrophic, nearly spherical, half immersed in the summit, followed by a regular dextral whorl. Mature whorls 10, short, flat, increasing regularly, the sutures marked by deep V-shaped channels, the body whorl with a sharp, spiral keel on the periphery, the base rounded, narrowly umbilicate. No sculpture; the surface smooth and polished. Aperture extended anteriorly, the outer margin straight, anterior margin straight, narrowly reflected, but sufficiently to nearly obscure the umbilicus, with a single strong fold, posteriorly situated. Length 8·5 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and two paratypes; 4–14 fm Albany Passage (C. Hedley).

Remarks.—By its short whorls, channelled sutures, and by its aperture this distinctive species comes within *Colsyrnola*, though the narrow umbilicus, the sharply angled body whorl, and the vitreous instead of porcellanous texture suggest it should be separated as another genus. From *C. sericea* it is readily separated by all these characters, by the colour, and by being relatively broader. The umbilicus is not easy to distinguish, being very narrow and partly or wholly hidden by the reflection of the inner margin of the aperture.

COLSYRNOLA MARGARITA, sp. nov.

Figs. 34 and 35

Shell large, conical, elongate, acuminate, colour cream, with a narrow, spiral, brown band just above the sutures and on the periphery of the body whorl, texture porcellanous. Protoconch anastrophic, planoid, tilted on the summit. Mature whorls 13, short, flat, sutures deeply channelled. Sculpture absent, surface smooth and polished. Aperture extended anteriorly, semicircular, outer and anterior margins rounded, inner margin curved, thickened, and reflected, a single oblique fold posteriorly placed, the reflection covering and obscuring what appears to be a very narrow umbilicus. Length 14 mm.

Locality.—North-west Island, Capricorn Group, holotype and one paratype.

Remarks.—From the other species of *Colsyrnola* here discussed, this species can readily be separated by its colouring, which actually approaches very closely the several species described under the generic name *Urambella*. The possibility of it being umbilicate, a character obscured by the overhang of the inner margin of the aperture, would indeed take it into *Urambella* were it not that there is only one columella fold instead of three. Compared with species of *Urambella*, in appearance it approaches closest to *U. affinis*, but it is still narrower.

COLSYRNOLA CANARIA (Hedley)

Figs. 36 (after Hedley) and 37

Odostomia canaria Hedley, 1907, p. 503, pl. 18, fig. 32.

The type locality is 17–20 fm off Masthead Island, Capricorn Group, the length of the type given as 2·35 mm. A copy of Hedley's figure is here given for reference (Fig. 36), and also a drawing of a single specimen from 4–14 fm Albany Passage (Fig. 37) which appears to be the same species. This is somewhat larger, 4·2 mm in length, has an extra whorl, and differs also in a few minor details. It is pale yellow in colour, and like the type is umbilicate. The colour of the type is given as a bright canary-yellow, and this should be a very useful guide in future recognition.

This species is very doubtfully referred to *Colsyrnola* as it is definitely umbilicate. There is, however, the likelihood that specimens so far examined, including the type, are immature, and but for the umbilicus, they might well be the young of *C. sericea*.

Genus SYRNOLA A. Adams

Type species by monotypy *Syrnola gracillima* A. Adams.
Syrnola A. Adams, 1860*a*, p. 405.

The shell is elongate and acuminate, vitreous, perfectly smooth, with a single, oblique columella fold, and, Adams states, with the sutures impressed. The type species came from Korea.

Many western Pacific shells fit this description, but owing to the simple characters it is hard to find any basis for tracing relationship. The texture of some species is porcellanous, and others are shorter and broader, approaching *Odostomia*. The sutures may be restricted, but they are not channelled as in *Colsyrnola*, and the columella fold is generally weak and oblique.

SYRNOLA PULCHRA Brazier

Fig. 38

Syrnola pulchra Brazier, 1877, p. 261.
Syrnola pulchra Brazier. Hedley, 1902, p. 125, pl. 16, fig. 20.

The type came from Darnley Island and is 5·5 mm long. The specimen here figured is from 5–10 fm Hope Island (C. Hedley), and is 6·6 mm long. It matches the type in every detail. A good recognition point is generally the brown spiral band just above the sutures on the earlier whorls and on the periphery of the body whorl, but this is not always apparent as it fades rapidly, leaving the specimens pure white. Other specimens from the Hope Islands are rather smaller, as are specimens from 5 fm Van Diemen's Inlet (C. Hedley), and others from 17–20 fm Masthead Island (C. Hedley).

The species is very close to *S. tincta* Angas, a Peronian species. The latter has been recorded from Queensland, but specimens so labelled appear to be faded examples of *S. pulchra*.

SYRNOLA SOLANDERIANA, sp. nov.

Fig. 39

Shell of medium size, regularly conical, elongate, broad at the base, tapering to an acute apex, white. Protoconch anastrophic, almost spherical, and partially immersed in about half the summit. Mature whorls 8, increasing regularly, short, nearly flat, not restricted at the sutures, which are marked by a very narrow groove.

Sculpture none, the surface smooth, porcellanous, and polished. Aperture extended anteriorly, outer margin flattened, anterior margin rounded, inner margin nearly straight, narrowly reflected, with a fairly prominent oblique fold, posteriorly situated. Length 6·2 mm.

Localities.—20 fm off Endeavour Reef (A. McCulloch), holotype; Bowen (J. Laseron); 11 fm Port Curtis (T. Iredale).

Remarks.—This species greatly resembles the southern *S. bifasciata* Tenison-Woods, but among other small differences lacks the double brown band of that species. Compared with *S. acerrima* (Watson) it has the same regular, conical, tapering spire, but is much larger and relatively much broader.

SYRNOLA ACERRIMA (Watson)

Fig. 40

Eulimella acerrima Watson, 1886, p. 496, fig. 3.

The type locality is 155 fm off Raine Island, the length of the type 0·11 in. (2·8 mm). The species is identified with some uncertainty as Watson's type was not quite mature and the outer margin of the aperture was broken. The species has not been recognized in material from adjacent localities, but a number of species from Darwin (J. Laseron) approximate very closely to Watson's figure and description. The one here figured is 4 mm, which, allowing for greater maturity, is close to the type.

A feature of the species is the regular, narrow, hardly tapering spire with barely impressed sutures. This is a typical *Syrnola*, a genus with which Watson was evidently unfamiliar. The columella fold is certainly weak and hardly visible from in front.

SYRNOLA TORRESIANA, sp. nov.

Fig. 41

Shell small, slender, elongate, spire narrow with slightly convex sides, white with a yellowish tinge, translucent. Protoconch exsert, anastrophic, initial whorls planoid, tilted on the summit. Mature whorls 8, very slightly rounded, sutures slightly impressed, body whorl narrowed towards the base in the type but not in all specimens. Sculpture none, the surface smooth and shining. Aperture extended anteriorly and in the type laterally (but the lateral extension is not present in all specimens), outer and anterior margins rounded, inner margin curved, narrowly reflected, with a small but distinct oblique fold posteriorly placed. Length 4·5 mm.

Localities.—4–14 fm Albany Passage (C. Hedley), holotype and numerous paratypes; Darwin (J. Laseron).

Remarks.—This is a common and rather variable species, particularly in the contour of the lower portion of the spire, a variation partially explained by the degree of maturity, and in the lateral expansion of the aperture. Some specimens are also relatively a little broader than the type and with fewer whorls.

SYRNOLA ERUCA, sp. nov.

Fig. 42

Shell minute, elongate, the lower two-thirds of the spire cylindrical, the upper third conical, white, translucent. Protoconch small, anastrophic, planoidly coiled, occupying about two-thirds of the summit. Mature whorls 6, the last 3 practically equal, relatively long, flat, sutures not impressed. Sculpture absent, the surface smooth and shining, texture slightly vitreous and translucent. Aperture extended anteriorly and slightly laterally, outer margin flat, anterior and inner margins rounded, the latter narrowly reflected, with a small but distinct oblique fold at the posterior extremity. Length 2·5 mm.

Locality.—15 fm Palm Islands (C. Hedley), holotype and 17 paratypes.

Remarks.—This is the smallest of the species here discussed, and the cylindrical form of the lower portion of the spire should facilitate its future recognition.

SYRNOLA CONVOLUTA (Watson)

Figs. 43 and 44

Odostomia convoluta Watson, 1886, p. 482, pl. 33, fig. 8.

The type locality is 7 fm Flinders Passage, the length of the type being given as 0·123 in. (3·1 mm). Figure 43 is from a series of specimens from 15 fm Palm Islands (C. Hedley), and approximates very closely to Watson's figure and description. It is 3·6 mm in length. Specimens from 5–10 fm Hope Islands (C. Hedley) are a little smaller, have one whorl less, and have the penultimate whorl swollen; also the aperture is more restricted anteriorly. It is not certain if these differences are sufficient to constitute a separate species or even race, but a specimen, 2·7 mm long, is here figured for future reference (Fig. 44).

The generic position of the species is also open to some doubt. The differences between the genera *Syrnola* and *Odostomia* are not always clearly defined, and this species lies on the borderline, with perhaps the balance in favour of *Syrnola*.

SYRNOLA EXSERTA, sp. nov.

Fig. 45

Shell of medium size, elongate, with very convex spire, the lower portion nearly cylindrical, slender at the summit, white, slightly translucent. Protoconch relatively large and tumid, exsert, anastrophic, the sinistral portion nearly spherical and at right angles to the axis, followed by an inflated, nearly straight, tubular whorl, gradually twisting dextrally. Mature whorls 7, very slightly rounded, not restricted at the sutures, the body whorl short. No sculpture, the surface smooth and shining. Aperture extended anteriorly, outer margin nearly straight, anterior margin rounded, inner margin curved, evenly reflected, with a single, moderately prominent oblique fold. Length 5 mm.

Localities.—Bowen (J. Laseron), holotype and one paratype; Lady Elliott Island (C. Hedley).

Remarks.—The highly convex spire and exsert protoconch, making the summit almost mamillate, are good recognition points for this species. It resembles most the southern species *Odostomia tasmanica* (Tenison-Woods), but has relatively a much shorter body whorl and more whorls.

Genus PARODOSTOMIA, gen. nov.

Type species *Odostomia compta* Brazier.

Shell like *Odostomia*, smooth and without sculpture, but angled at the periphery, and with deeply channelled sutures. The single fold on the inner margin of the aperture is also strong and nearly transverse.

Parodostomia will replace the use of *Scalenostoma* Deshayes (1863, p. 58) for certain Australian and possibly New Zealand shells. The monotype of *Scalenostoma* is *S. carinatum* Deshayes from Réunion in the Indian Ocean. This is a very peculiar shell, with concave whorls, a prominent narrow keel on the periphery of the body whorl and sutures, no columella fold, and it is very doubtful whether it belongs to the Pyramidellidae at all. Of the two west American species assigned to *Scalenostoma*, *S. rangii* (de Folin) might be congeneric, the other, *S. dotella* Dall & Bartsch, is apparently a *Parodostomia*. Among southern Australian species *S. subcarina* Laseron and *S. pyramidata* Laseron will now be transferred to *Parodostomia*.

PARODOSTOMIA COMPTA (Brazier)

Figs. 46–48

Odostomia compta Brazier, 1877, p. 259.
Odostomia affinis Brazier, *O. polita* Brazier, *O. parvula* Brazier, 1877, pp. 259–60.
Odostomia compta Brazier, with vars. *affinis*, *polita*, and *parvula* Brazier. Hedley, 1901, p. 125, pl. 16, figs. 16, 17, 19, pl. 17. fig. 18.

The type of *compta* came from Darnley Island, *polita* and *parvula* from the same locality, and *affinis* from Cape York. The length of the type of *compta* is 5·5 mm, of *affinis* 5 mm, of *polita* 4 mm, and of *parvula* 3 mm.

Brazier described and proposed four separate species, but Hedley, who figured the types of the *Chevert* Expedition, came to the conclusion that all were merely varieties of the one species, though he retained Brazier's other names as varietal. Examination of long series from localities as far apart as Darwin, 14 fm Albany Passage, and Port Curtis confirms Hedley's views, and as the variation occurs indiscriminately in each locality, it is concluded that it is not even racial, and that the varietal names should be discarded.

The species is indeed variable, in size, number of whorls, relative width, and the prominence of the peripheral keel, which is barely discernible on some specimens. Some specimens are also hollowed at the base, forming a shallow, false umbilicus. The whorls are also at times nearly flat, at others slightly rounded. All, however, have a V-shaped channel at the sutures, similar protoconchs, the single columella fold is generally strong and transverse, and they are striated within the outer margin of the aperture. All intermediate stages between the extremes have been observed. Three specimens are here figured which show about the extremes of variation, but which, as to be expected, do not match the varieties figured by Hedley. Figure 46 is from 4–14 fm Albany Passage (C. Hedley), length 6·6 mm, Figure 47 from the same locality, 3·7 mm, and Figure 48 from Port Curtis, length 6 mm. Many specimens are under 3 mm in length.

Genus ODOSTOMIA Fleming

Type species *Turbo plicatus* Montagu.
Odostomia Fleming, 1817, p. 76.

From figures and descriptions of the type, *Odostomia* includes conical shells with relatively few whorls, from 3 to 7, with sinistral protoconchs, rounded whorls which are entirely smooth and without sculpture, and a single columella fold, which in the type is prominent, but in many species is weak and only visible within the aperture.

Many authors, however, have used it in a much wider sense to include a large assembly of species, both smooth and sculptured, basing the generic connection solely on the single columella fold. Brazier, Tate, May, and Hedley used it thus for Australian species, and Watson for the material gathered by the *Challenger* Expedition. In America Dall and Bartsch used it both as a genus and a subgenus, the subgenus being one of 40 and conforming to the original generic description. Laws (1939), reviewing the New Zealand Pyramidellidae, refers to the odostomid group of genera, using full genera instead of subgenera for the various groups. This in effect is the course pursued by Dall and Bartsch. Laseron (1951) also used *Odostomia* as but one of many genera, but in the present paper, instead of referring to the "odostomid group of genera" the substitution of a subfamily Odostomiinae should simplify the nomenclature.

Even with the restriction of *Odostomia* within the limits of the description given, it is by no means certain that all the species discussed are closely enough related to be considered congeneric, but at least the characters given are definite enough for immediate taxonomic purposes. Later research into the animals and life history may well show that further subdivision is necessary.

The use of *Puposyrnola* Cossmann for certain living species needs to be reviewed. Laws used *Puposyrnola* for some New Zealand species and Laseron used it for Peronian species with large body whorls, which are inflated and generally longer than *Odostomia* s.s., with convex spire and apertures restricted at the anterior end. Reference to the original description of *Puposyrnola* Cossmann shows that the type species (1921, pl. 5, fig. 60) is a European Eocene fossil, narrow and pupoid in shape, and quite unlike any living Australian species. Pending additional data, such Peronian species as *Puposyrnola tasmanica* (Tenison-Woods) and *P. proletare* Laseron are better transferred provisionally to *Odostomia*.

The protoconch of many species of *Odostomia* is typically anastrophic like other members of the family, but in some species its sinistral character is obscured, either because the initial sinistral nucleus is very minute, or because the whole protoconch is twisted downwards to become immersed in the summit. It is doubtful, however, if the use of the protoconch is greater than for specific determination.

ODOSTOMIA CORPULENTA Watson

Fig. 49 (after Watson)

Odostomia corpulenta Watson, 1886, p. 484, pl. 31, fig. 3.

The type locality is 6 fm off Cape York, the length given 0·194 in. (almost 5 mm). It has not yet been reidentified. A copy of Watson's figure is here given, which shows it to resemble *O. clara* Brazier. However, it has a more convex spire, less rounded whorls, and the aperture is narrowed at the anterior end.

ODOSTOMIA RECTA, sp. nov.

Fig. 50

Shell of medium size, conical, narrow, elongate, spire slightly convex, white. Protoconch anastrophic, small, nearly spherical, and folded within the summit. Mature whorls 6, long, nearly flat, sutures not impressed, body whorl long and cylindrical, about half the total length. No sculpture, the surface smooth, shining, and translucent. Aperture long, extended and narrowed anteriorly, outer margin flat, anterior margin rounded, inner margin rounded with a single, strong oblique fold. Length 5 mm.

Locality.—1–3 fm Port Curtis (J. Laseron), holotype.

Remarks.—The long, narrow body whorl and flattened whorls make this species distinctive, and it cannot readily be confused with any other here discussed.

ODOSTOMIA CLARA Brazier

Fig. 51

Odostomia clara Brazier, 1877, p. 259.
Odostomia clara Brazier. Hedley, 1901, p. 125, pl. 16, fig. 15.

The type is from Darnley Island, the length given being 5·5 mm. The specimen figured is from the Barrier Reef off Cairns (D. Pitt), and is 4·5 mm long, rather smaller than the type, but otherwise conforming in all details. A character shown in the original figure is striations within the outer margin of the aperture. This has been observed in some but not all specimens. A long series from 20 fm off Endeavour Reef (A. McCulloch) shows some variation within narrow limits, both in size and form. The species has also been collected from 4–14 fm Albany Passage (C. Hedley), Darwin (J. Laseron), and Keppel Bay (J. Laseron).

ODOSTOMIA OXIA Watson

Figs. 52 and 53 (after Hedley)

Odostomia oxia Watson, 1886, p. 484, pl. 31, fig. 4.
Odostomia adipata Hedley, 1909, p. 444, pl. 42, fig. 73.

Watson's type came from 7 fm Flinders Island, Hedley's from 5–10 fm Hope Islands. Figures and descriptions of *oxia* and *adipata* agree in all essential details, and specimens examined from Darwin (J. Laseron) and Barrier Reef off Cairns (D. Pitt) could readily be assigned to either name. It seems, therefore, that *adipata* is a synonym of *oxia* and must give place to it. Figure 52 is from a Darwin specimen, 2·1 mm in length, Figure 53 is copied from Hedley's original figure, the length given being 1·9 mm.

This is a solid little species, smooth, shining, and subtranslucent.

ODOSTOMIA ADIPOSA, sp. nov.

Figs. 54 and 55

Shell minute, solid, broadly conical, anteriorly inflated, white. Protoconch small, anastrophic, almost spherical, half immersed in the summit. Mature whorls 4, increasing rapidly, the body whorl relatively large and inflated, about two-thirds of the total length, the whorls slightly rounded and restricted at the sutures. No sculpture, the surface smooth and polished. Aperture not extended anteriorly, the outer and anterior margins rounded, inner margin rounded and narrowly reflected, with a distinct oblique fold at the posterior end. Length 2·3 mm.

Localities.— 4–14 fm Albany Passage (C. Hedley), holotype (Fig. 54) and one paratype; Darwin (J. Laseron) (Fig. 55); Barrier Reef off Cairns (D. Pitt); Heron Island (J. Voorwinde).

Remarks.—Throughout this considerable range this is a constant little species, varying only slightly in size, the Darwin and Cairns specimens being slightly larger than the type, and that from Heron Island smaller. The broad, regularly conical form, and large body whorl should facilitate future recognition.

ODOSTOMIA MERA, sp. nov.

Fig. 56

Shell minute, narrowly conical, spire with little taper and a blunt apex, solid, white, and translucent. Protoconch anastrophic, nearly spherical, and infolded in the summit. Mature whorls 4, long, nearly flat, not restricted at the sutures, the body whorl long and about half the total length. No sculpture, the surface smooth and shining. Aperture extended anteriorly, outer margin slightly rounded, anterior margin rounded, inner margin curved and reflected, with a single, oblique, relatively strong fold at the posterior end. Length 2 mm.

Localities.—Darwin (J. Laseron), holotype and one paratype; 20 fm off Endeavour Reef (A. McCulloch).

Remarks.—This is a distinctive little species, readily recognizable by its form. No difference is discernible between specimens from the two known localities even though these are geographically wide apart.

ODOSTOMIA sp.

Fig. 57

A single specimen from Keppel Bay (J. Laseron) is almost certainly an undescribed species, but in view of the variability of some species of *Odostomia* it is thought advisable to leave it unnamed until further material is available. By its flattened whorls, conical spire, and blunt apex it resembles *O. mera*, but it is larger, 3 mm in length, relatively much broader at the base, and with a more rapid taper.

The colour is white, it is slightly translucent, and the surface is polished. It is here figured for future reference. A second specimen from Bowen (J. Laseron) is probably the same species, though smaller (only 2·2 mm in length).

ODOSTOMIA METATA Hedley

Fig. 58 (after Hedley)

Odostomia metata Hedley, 1907, p. 503, pl. 18, fig. 35.

This species has not yet been rediscovered, but from Hedley's excellent figure and description it should be easy to recognize, particularly by the colour pattern of chocolate on a cream ground, and by the form. The type locality is 17–20 fm, Masthead Island, Capricorn Group, the length given 2·35 mm.

ODOSTOMIA SPERABILIS Hedley

Fig. 59 (after Hedley)

Odostomia sperabilis Hedley, 1909, p. 448, pl. 41, fig. 71.

The type locality is 5–10 fm Hope Islands, and other localities given are the Palm Islands and Masthead Island. The length of the type is 3 mm. The species has not yet been reidentified from material from these localities, but the figure shows a subcylindrical shell of irregular growth, with swollen, well-rounded penultimate and antepenultimate whorls, and a complete peristome, the last character not mentioned in the description. The description on the other hand speaks of irregularly disposed varices which are not shown in the figure. Until further material is available these discrepancies make the status of the species uncertain.

ODOSTOMIA ABJECTA Hedley

Figs. 60 (after Hedley), 61, and 62

Odostomia abjecta Hedley, 1909, p. 444, pl. 41, fig. 62.

The type locality is 5–10 fm, Hope Islands, the length given 1·65 mm. There is some uncertainty as to the identification of this species. A character mentioned in the description and shown in Figure 60 is that the aperture is bent in towards the axis, but this has not been observed in any other material examined. Specimens nearest to *abjecta* are from 4–14 fm Albany Passage (C. Hedley) and from the Palm Islands (C. Hedley). Figure 61 is from the Albany Passage and is 2 mm long. It shows some differences from the figure of the type, and though tentatively identified as *abjecta*, it may possibly be another undescribed species. A number of specimens from the Palm Islands are identical with those from Albany Passage, but one apparently abnormal specimen has added an additional whorl after a slight break. It is here figured for comparison and is 3·4 mm long (Fig. 62).

ODOSTOMIA STRICTA, sp. nov.

Fig. 63

Shell of medium size, ovate in contour, broad, spire with convex sides, solid, white and opaque. Protoconch small, anastrophic, infolded in summit. Mature whorls 5, increasing rapidly, well rounded and deeply restricted at the sutures, the penultimate whorl large and inflated, body whorl about half the total length. No sculpture, the surface smooth and rather dull. Aperture extended anteriorly, nearly round, all the margins rounded, the inner margin short and narrowly reflected, the single fold slight, oblique, at the posterior extremity, and barely visible from in front. Length 4·8 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype; 4–14 fm Albany Passage (C. Hedley); Darwin (J. Laseron).

Remarks.—The form, well-rounded whorls, and deep sutures are good recognition points of this distinctive species. The specimen from Albany Passage is a little smaller, but otherwise matches the type. Specimens from Darwin are again a little smaller and narrower, but otherwise conform, though far apart geographically.

ODOSTOMIA ERUCA, sp. nov.

Fig. 64

Shell large for the genus, elongate, of rather irregular growth, white and shining. Protoconch anastrophic, small, prostrate on summit, of 2 whorls, the second inflated. Mature whorls 7, long, of irregular growth, at first increasing regularly, the antepenultimate and penultimate whorls equal, the body whorl relatively large and swollen, the whorls well rounded and restricted at the sutures. Sculpture none, the surface smooth and polished. Aperture extended anteriorly, outer and anterior margins rounded, inner margin curved, long, narrowly reflected, with a single, slight, very oblique fold. Length 8 mm.

Locality.—Brampton Island, holotype.

Remarks.—This is the largest and most elongate of the species discussed. The rounded whorls and restricted sutures are similar to *O. stricta*, but it is much larger, relatively narrower, and the whorls are longer.

ODOSTOMIA ANXIA Hedley

Fig. 65 (after Hedley)

Odostomia anxia Hedley, 1909, p. 444, pl. 41, fig. 63.

The type locality is 5–10 fm Hope Islands, the length given 1·95 mm. This is a minute species which has not been further identified since Hedley's description. Its peculiar and distinctive form should make its eventual recognition easy, and might indeed eventually justify generic separation.

ODOSTOMIA BULBULA Hedley

Fig. 66 (after Hedley)

Odostomia bulbula Hedley, 1907, p. 504, pl. 18, fig. 34.

The type locality is 17–20 fm Masthead Island, Capricorn Group, the length given 3·5 mm. Though known only from a single specimen, the very distinctive form again separates this species from all others here discussed, and might further eventually justify generic separation.

Genus HINEMOA Oliver

Type species *Hinemoa punicea* Oliver.
Hinemoa Oliver, 1915, p. 531.

The type species came from the Kermadecs. The original description reads: "ovate, protoconch 1-whorled, aperture ovate, columella with a feeble plait, sculpture of spiral ribs only". To this can be added that the type is a minute shell, only 1 mm in length, with only 4 whorls, and is uniformly red in colour.

A closely allied southern Australian shell which is undoubtedly congeneric, *Parthenia tasmanica* Tenison-Woods, was placed in *Oscilla* A. Adams by Hedley, and other allied species from the Hope Islands, Queensland, were simply described by Hedley as *Odostomia*.

Reference to *Oscilla* shows that confusion has arisen as to the actual type species. Most subsequent authors give the date of the introduction by Adams of *Oscilla* as 1867 (p. 310). Adams then listed five species, the first of which was *lirata* A. Adams from Japan, and this has been accepted as the type. But Iredale (1910, p. 54) points out that Adams introduced *Oscilla* in 1861 (p. 296), where he clearly designated a type when he described *Monoptygma cingulata* from China, and stated: "this species is by no means typical and should form a subgenus under the name *Oscilla*". The description of *cingulata* shows a shell with similar sculpture to *Hinemoa*, but larger, with many more whorls (7½ actually), elongate (the description says "testa turrito sub-subulata"), more in fact like a *Cingulina*, but with a fold on the columella.

Hinemoa can therefore be taken as quite separate from the true *Oscilla*, and it covers what seems a natural group of south-western species.

HINEMOA GUMIA (Hedley)

Fig. 67

Odostomia gumia Hedley, 1909, p. 446, pl. 41, fig. 67.

The type locality is 5–10 fm Hope Islands, the length given 3·55 mm. Characteristics are the conical form, rather acute apex, 3 equal spiral ribs on the earlier whorls and 8 on the body whorl. It is reidentified with a little uncertainty, as available material is not in the best of condition. A specimen from 4–14 fm Albany Passage (C. Hedley) is, however, close to Hedley's figure and description, and is here figured; its length is 2·5 mm, rather smaller than the type. Other specimens are from the Barrier Reef off Cairns (D. Pitt).

HINEMOA MIGMA (Hedley)

Fig. 68

Odostomia migma Hedley, 1909, p. 447, pl. 41, fig. 70.

The type locality is 5–10 fm Hope Islands, the length of the type given as 3·55 mm. Again this is reidentified with a little uncertainty, as specimens now attributed to this species are less angled at the periphery of the body whorl and not so flat on the base as is shown in the original figure. It is a longer and narrower species than *H. gumia* (Hedley). The specimen here figured is from 4–14 fm Albany Passage (C. Hedley) and is 3·2 mm long. Other specimens placed here are from Darwin (J. Laseron).

HINEMOA STERNEREA, sp. nov.

Fig. 69

Shell small, but large for the genus, broadly and regularly conical with an acute apex, colour pale cream. Protoconch small, anastrophic, half immersed in the summit. Mature whorls 4, increasing regularly and rapidly, the body whorl large, flattened, deeply but narrowly channelled at the sutures. Sculpture of heavy, broad, raised spiral ribs separated by narrow but deep channels, 3 on the early whorls, 7 on the body whorl, the basal ribs becoming smaller, the upper rib on the body whorl flattened and showing signs of becoming bifurcate, the channels between the ribs obliquely striate. Aperture extended laterally but only slightly anteriorly, the outer and anterior margins rounded and indented by the sculpture, inner margin curved and narrowly reflected, the single fold slight and oblique, barely visible from in front. Length 4 mm.

Locality.—11 fm Port Curtis (T. Iredale), holotype and seven paratypes.

Remarks.—This is a distinctive species, larger and relatively much broader than any other here discussed. It is closest to *H. migma* (Hedley), but is much broader, has the aperture more laterally expanded, and has a smaller and more deeply immersed protoconch.

HINEMOA LAQUEARIA (Hedley)

Fig. 70 (after Hedley)

Odostomia laquearia Hedley, 1909, p. 447, pl. 43, fig. 82.

The type locality is 5–10 fm Hope Islands, the length of the type given 1·4 mm. This minute species has not been reidentified, and there is a discrepancy between the published figure and description. The description states that the three whorls have respectively 2, 3, and 6 spiral ribs, whereas the figure shows 3, 4, and 8. Examination of the type in the Australian Museum shows that the figure can be taken as correct, and as a true portrayal of the characters of the species.

HINEMOA RUBRA, sp. nov.

Fig. 71

Shell minute, ovately conical, solid, colour a uniform bright brown-red. Protoconch anastrophic, of 2 whorls, prostrate on the summit. Mature whorls apparently 3, flattened, the sutures indistinguishable from the furrow between the ribs. Sculpture of strong, wide, raised, rounded spiral ribs, separated by deep narrow channels, 11 in all, apparently 3 each on the first two whorls and 5 on the body whorl, the two basal ribs weaker than the others. Aperture slightly extended and narrowed anteriorly, the outer margin indented by the sculpture, anterior margin rounded, inner margin curved and narrowly reflected, the single fold slight and invisible from in front. Length 1·6 mm.

Localities.—Alive under coral blocks Heron Island, Capricorn Group (J. Laseron), holotype and three paratypes; 34 ft Gannet Passage, Torres Straits.

Remarks.—Apart from the minute size and sculpture the bright red-brown colour distinguishes this from other northern species. It is very close to the type species *H. punicea* Oliver from the Kermadec Islands, but the ribs are larger and closer together.

HINEMOA DUPLEX, sp. nov.

Fig. 72

Shell small, solid, broadly conical with a narrow apex, white. Protoconch anastrophic, nearly spherical, half immersed in summit. Mature whorls 5, flattened, the sutures channelled, but barely distinguishable from the channels between the spiral ribs. Sculpture of strong, rounded spiral ribs, separated by deep channels, 2 equal ribs on the first whorl. On the second whorl the upper rib begins to bifurcate, and on the last two whorls divides into two, separated by an incised line. Including these the body whorl has 6 ribs, becoming weaker on the base. Aperture slightly extended anteriorly, outer margin rounded and narrowed anteriorly, indented by the sculpture, inner margin curved and reflected, with a single, strong, nearly transverse fold. Length 2·9 mm.

Localities.—4–14 fm Albany Passage (C. Hedley), holotype; 15–20 fm Pt. Charles, Darwin (M. Ward).

Remarks.—The peculiar sculpture, with the gradual bifurcation of the upper spiral rib, is a good distinguishing character for this species.

HINEMOA LEVIPLEX, sp. nov.

Fig. 73

Shell small, ovately conical, white. Protoconch very small, probably anastrophic, appearing as an almost spherical ball, half immersed in about half the summit. Mature whorls 4, rounded, restricted at the sutures, rather long, the body whorl long, about half the total length. Sculpture of rounded spiral ribs, 4 to the whorl, about their own width apart, with an additional narrow rib at the sutures, the body whorl with about 9 ribs, becoming weaker on the rounded base, the furrows between the ribs crossed by oblique axial threads. Aperture well extended anteriorly, the outer and anterior margins thin and indented by the sculpture, the inner margin long, nearly straight, narrowly reflected, with no visible fold. Length 3·6 mm.

Locality.—11 fm Port Curtis (T. Iredale), holotype.

Remarks.—Though the sculpture conforms to *Hinemoa*, the rounded whorls and absence of a columella fold suggest that it may have other relationship, and it may ultimately have to be removed from that genus.

HINEMOA VOORWINDEI, sp. nov.

Fig. 74

Shell minute, broadly ovate, with a very convex spire, white. Protoconch anastrophic, nearly planoid, tilted on summit. Mature whorls 4, very slightly rounded, parted by deep sutures, deeper than the grooves between the spiral ribs.

Sculpture of well-defined, rounded spiral ribs, less than their own width apart, 3 on the first two whorls, 4 on the penultimate, and about 11 on the body whorl, the ribs becoming smaller on the rounded base. Aperture well extended anteriorly, outer and anterior margins thin and rounded, indented by the sculpture, inner margin long, curved, narrowly reflected, with a small but distinct oblique fold posteriorly placed. Length 2 mm.

Locality.—6–25 ft Heron Island, Capricorn Group (J. Voorwinde), holotype and four paratypes.

Remarks.—Compared with most other species of *Hinemoa* this can readily be separated by the convex form and more numerous and narrower spiral ribs. By the last character it somewhat resembles *H. leviplex*, but is smaller, has a different form and a distinct columella fold. It is named after Mr. J. Voorwinde who not only collected the species but has sorted out much small material for this paper.

HINEMOA sp.

Fig. 75

Two specimens dredged off Pt. Charles, Darwin (M. Ward), are certainly one and possibly two undescribed species. Both have broken apertures and may not be mature, and more and better material is needed before they can be adequately described and named. The larger of the two, 4·5 mm in length, is here figured for future reference. It is an elongated, conical shell, with 6 whorls, and strong spiral ribs, 3 to the whorl. The sutures are distinguishable by being deeper than the furrows between the ribs. The badly broken aperture shows a single strong fold encircling the columella, but in the unbroken shell this would probably not be so conspicuous from in front. The second specimen is only about half the size, with as many whorls, is relatively more slender, but has identical sculpture. The nearest comparative species is *H. migma* (Hedley).

HINEMOA FOSSALINA, sp. nov.

Fig. 76

Shell small, solid, conical, with slightly convex sides, apex obtuse, colour a uniformly pale yellow. Protoconch large, smooth, domed, the nucleus immersed in the summit. Number of whorls uncertain, as the sutures are indistinguishable, but probably 4. Sculpture of very broad, nearly flat spiral ribs, separated by little more than incised lines, 9 ribs in the whole of the spire, base of body whorl rounded and smooth. Aperture slightly extended anteriorly, a layer of callus on the body whorl within, outer margin indented by the sculpture, anterior margin narrowed, making an angle with the inner margin, which is curved and reflected, with a single, very strong, nearly transverse fold. Length 4 mm.

Locality.—Sweers Island (C. Hedley), holotype.

Remarks.—Very little collecting has been done in the Gulf of Carpentaria, and the odd specimen from that area nearly always is revealed as a striking new species. This unique species is an example. It is tentatively placed in *Hinemoa*, as it agrees with the generic description, but the broad, nearly flat, spiral ribs, in two series, alternately very wide and slightly narrower, give it such a distinct facies, that further material and the discovery of allied species will almost certainly necessitate its removal to a new genus.

Genus EVALEA A. Adams

Type species *Evalea elegans* A. Adams.
Evalea A. Adams, 1860*b*, p. 22.

Shell like Odostomia, but instead of being smooth, having sculpture of fine, incised spiral lines. The type species comes from Japan.

EVALEA QUEENSLANDICA, sp. nov.

Fig. 77

Shell of medium size, conical, elongate, with a slightly convex spire, the first three whorls pink, remainder white. Protoconch anastrophic, exsert, planoidally coiled, tilted on summit. Mature whorls 6, increasing regularly, long, very slightly rounded, and not restricted at the sutures, body whorl long. Sculpture absent on the early whorls, the lower whorls under an ordinary lens smooth, but higher magnification shows numerous fine spiral striations with a few faint axial plications at the summits of the whorls. Aperture slightly extended anteriorly, the outer and anterior margins rounded, the inner margin rounded and narrowly reflected, with a faint, oblique fold, posteriorly situated and barely visible from in front. Length 5·7 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype and numerous paratypes; Green Island, Cairns (C. Hedley); Masthead Island (C. Hedley).

Remarks.—This is the species which has previously been known from various localities in the western Pacific as *Odostomia rubra* Pease. Dall and Bartsch (1904, p. 6) made *O. rubra* the type of their subgenus *Syrnolina*, a characteristic of which, apart from both axial and spiral striations, is a strong spiral keel at the summits of the whorls. Reference to the original description of *rubra* by Pease (1867, p. 291, pl. 24, fig. 18), the type of which came from the Paumotu Archipelago, also shows a narrow, elongate shell without a columella fold, which brings *Syrnolina* within the Turbonillinae and not the Odostimiinae, so that the present species differs not only specifically, but generically, and is within a different subfamily. The fine spiral striations bring *queenslandica* into *Evalea*, though the sculpture disappears with the slightest wear. The pink early whorls, which sometimes fade to yellow, are a good recognition point. Apart from the Queensland localities, the species has a wide range, and specimens from New Caledonia, Lifu, and Fiji show very little variation.

Genus KUNOPIA, gen. nov.

Type species *Odostomia sigma* Hedley.

A minute shell described by Hedley from Masthead Island has distinctive characters which do not permit its inclusion in any other hitherto recognized group. These are its minute size, broadly conical form, few whorls, greatly enlarged body whorl, the sinuate sides of the whorls and the outer margin of the aperture, and the sinuate, very oblique sculpture of fine axial cords or threads.

Kunopia sigma (Hedley)

Fig. 78 (after Hedley)

Odostomia sigma Hedley, 1907, p. 504, pl. 18, fig. 33.

This species was based on a single specimen from 17–20 fm, Masthead Island, Capricorn Group, its length given as 2·3 mm. It has not since been reidentified, but its characters, both specific and generic, are so distinctive that there should be no difficulty in its future recognition.

Genus HERVIERA Melvill & Standen

Type species *Pyrgulina gliriella* Melvill & Standen.
Herviera Melvill & Standen, 1899, p. 185.
Rugadentia Laseron, 1951, p. 309, synonym.

Shell like *Elodiamea*. but with a nearly oval shell, aperture with a short inner margin and complete peristome, the single columella fold weak. Shells often coloured or with coloured bands. *Herviera* seems a compact and natural genus, of which there are several species in Queensland. The type species came from Lifu.

When *Rugadentia* was described Melvill's and Standen's paper was overlooked, and it is now withdrawn as a synonym of *Herviera*. The two Peronian species *Rugadentia ignava* (Hedley) and *R. doliae* Laseron will therefore be transferred to *Herviera*.

Herviera gliriella (Melvill & Standen)

Fig. 79

Pyrgulina gliriella Melvill & Standen, 1896, p. 303, pl. 10, fig. 57.

The type locality is Lifu, the length given 2·25 mm. The species is identified with a little uncertainty. The specimen figured is from Bowen (J. Laseron), is a bright deep red purple in colour, and is 2·7 mm in length. It agrees well with the original description and reasonably well with the rather poor figure, but only actual comparison with authentic specimens can verify the identification. Specimens from 5–10 fm Hope Islands (C. Hedley) are a little smaller and relatively slightly narrower than that figured, and their colour is partially faded. Another specimen is from 4–14 fm Albany Passage (C. Hedley).

Herviera chorea (Hedley)

Fig. 80 (after Hedley)

Odostomia chorea Hedley, 1909, p. 445, pl. 41, fig. 66.

The type locality is 5–10 fm Hope Islands, the length given 2 mm. From the description and figure this is a typical *Herviera*, the form and complete peristome being characteristic. It has not been reidentified, but the minute size and colour pattern, like *Elodiamea fasciata*, white with a narrow, peripheral yellow band, should make its future recognition easy.

Herviera sp.

Fig. 81

A single specimen from 20 fm off Endeavour Reef (A. McCulloch) is here figured for future reference. It is 2·7 mm in length. It is very like *H. chorea* (Hedley), except that the axial ribbing is coarser, and the colour is white without the yellow spiral band. More material is needed to decide if it is a distinct species or merely a colour variety of *H. chorea*.

HERVIERA PUPA (Watson)

Fig. 82 (after Watson)

Odostomia pupa Watson, 1886, p. 486, pl. 31, fig. 7.

The type locality is 7 fm Flinders Passage, the length given 0·13 in. (3·3 mm). The species has not as yet been reidentified, but its few and very weak axial ribs should facilitate its future recognition. The texture is given as porcellanous.

HERVIERA MAGIS, sp. nov.

Fig. 83

Shell of moderate size (but very large for the genus), ovate, elongated, with a slightly convex spire, colour of type white, but occasionally with faint brown spiral bands. Protoconch large, anastrophic, nearly spherical, tilted on summit. Mature whorls 6, increasing regularly, slightly rounded but hardly restricted at the sutures, body whorl relatively long. Sculpture of numerous, closely packed, low, rounded axial ribs, about 30 to the whorl, continuous but faint on the base. Just below the sutures the ribs are bent slightly inwards to produce a continuous shallow sulcus. Aperture anteriorly extended, all margins rounded, the inner margin thickened anteriorly, the single fold slight and oblique, barely visible from in front, the peristome complete, but narrow, adjoining the body whorl. Length 8 mm.

Localities.—Lindeman Island (T. Iredale), holotype; Palm Islands (C. Hedley); Murray Island.

Remarks.—There is no other species with which this can readily be compared. It is provisionally placed in *Herviera*, as the complete peristome and sculpture conform to that genus, but its large size, *Rissoina*-like appearance, and the shallow sulcus below the sutures suggest that it has other relationship.

Genus ELODIAMEA Hoyle

Type species *Elodia elegans* de Folin & Perier.
Elodia de Folin & Perier, 1875, p. 175, pl. 7, fig. 1.
Elodiamea Hoyle, 1885, nom. nov. for *Elodia* (preocc.), *Zool. Rec.* Vol. 22, p. 94.

For short odostomiid genera with sculpture of rounded axial ribs and no spiral sculpture there are several generic or subgeneric names available.

Dall and Bartsch (1904) in their key discriminate between *Elodiamea* with shell inflated, summits of whorls slightly shouldered, *Odostomiella* (*sic* = *Odostomella*) Bucquoy, Dautzenberg, & Dollfus (1883, p. 167), type *Rissoa doliolum* Philippi, shell not inflated, summits of whorls not shouldered; and *Salassia* de Folin (1885, p. 223), type *Salassia carinata* de Folin, with shell not inflated and summits of whorls tabulated. Dall and Bartsch (1909, p. 133) added *Salassiella*, type *Salassiella laxa* Dall & Bartsch, as having an inflated shell, axial ribs extending to the base, and irregularly distributed strong varices.

The reference to *Salassia* de Folin by Dall and Bartsch is not quite correct. De Folin and Perier first used the name *Salassia carinata* as a nomen nudum (1871, p. 314). They later (1875, p. 168, pl. 6, fig. 6, footnote, dated May 1872) described and figured the same species from Panama. In the same volume they described *Salassia daguaneti* (p. 112, pl. 3, fig. 2). If the earlier nomen nudum be rejected, then *Salassia daguaneti* by page priority becomes the type of *Salassia*. This is a rather nondescript species from Cape Breton in France and bears no resemblance to any Pacific form. Further confusion is caused by Dall and Bartsch (1909, p. 134) proposing a new specific name *tropidita* for *Salassia carinata*, as being preoccupied by *Odostomia carinata* A. Adams and *Scalenostoma carinata* Deshayes. As all three species were proposed under different generic names, as long as the genera are considered valid, so must the specific names. *Salassia tropidita* Dall & Bartsch must therefore be rejected as an absolute synonym of *S. carinata* de Folin & Perier.

Of the groups above listed *Elodiamea* most nearly covers what seems a natural group of eastern Australian shells. The type *Elodia elegans* came from Hong Kong, and its characters approximate very closely to many Australian shells. Discrimination might possibly be made between those with a weak and those with a strong columella fold, but the division is not clearly marked. Differences between the species are otherwise the number and strength of the axial ribs, the form, the size, and occasionally the protoconch.

ELODIAMEA KYMATODES (Watson)

Fig. 84

Odostomia kymatodes Watson, 1886, p. 486, pl. 31, fig. 8.

The type locality is 7 fm Flinders Passage. The species is easily recognizable from Watson's figure and description, and it is abundant in the nearby locality 4–14 fm Albany Channel (C. Hedley). The specimen illustrated is from there and its length is 3 mm. Watson states his specimens to be rather worn, and their colour is white, but in the long series examined fresh specimens are a uniform yellow-brown, while others have faded to white. It is constant in its characters, except that some specimens are a little narrower than the one figured.

ELODIAMEA FASCIATA, sp. nov.

Fig. 85

Shell small, ovate, inflated, with a convex spire, colour very pale amber, with a narrow spiral band of bright orange on the centre of each whorl, with an additional band on the base of the body whorl. Protoconch anastrophic, small, prostrate on the summit, of 2 whorls, the second inflated. Mature whorls 6, very slightly rounded and hardly restricted at the sutures. Sculpture of strong, rounded axial ribs, less than their own width apart, 16 to the whorl, persistent on the base. Aperture extended anteriorly, slightly narrowed anteriorly, outer margin slightly rounded, anterior margin rounded, inner margin nearly straight, with a single oblique fold. Length 3·2 mm.

Localities.—Caloundra (J. Laseron), holotype and two paratypes; Barrier Reef off Cairns (D. Pitt).

Remarks.—This species is very closely related to *E. kymatodes* (Watson), but has fewer and stronger axial ribs, and can readily be separated by the distinctive colour pattern. The colour pattern is in fact identical with that of *Herviera chorea* (Hedley), which, however, is much narrower, and has a complete peristome which takes it into a different genus.

ELODIAMEA ORA, sp. nov.

Fig. 86

Shell small, broadly conical, the spire slightly convex, white. Protoconch apparently anastrophic, but the sinistral portion infolded in the summit, followed by a relatively large, short, smooth dextral whorl. Mature whorls 4, increasing rapidly, rounded, restricted at the sutures, the body whorl large, about half the total length. Sculpture of strong, rounded, slightly oblique axial ribs, about their own width apart, about 20 to the whorl, continuous on the base. Aperture slightly extended anteriorly, outer and anterior margins rounded, inner margin curved, reflected, with a single, strong, nearly transverse fold. Length 3·5 mm.

Localities.—Keppel Bay (J. Laseron), holotype; 1–3 fm Port Curtis (J. Laseron), abundant; Barrier Reef off Cairns (D. Pitt), abundant.

Remarks.—Compared with both *E. kymatodes* and *Herviera chorea* this is a wider and less convex shell, the protoconch is different, the axial ribs are more numerous, and the columella fold much larger and well apparent from in front.

ELODIAMEA CADUCA, sp. nov.

Figs. 87 and 87(*a*)

Shell of medium size, large for the genus, broadly conical with a slightly convex spire, white. Protoconch large, anastrophic, nearly spherical, tilted on summit. Mature whorls 5, increasing rapidly, rounded and deeply restricted at the sutures, the body whorl relatively large, swollen, about half the total length. Sculpture of numerous rounded axial ribs, about their own width apart, about 22 to the whorl, more prominent at the summits of the whorls and fading on the lower parts and on the base of the body whorl. Aperture extended and narrowed anteriorly, outer margin rounded, inner margin curved and narrowly reflected, the single fold very slight and oblique. Length 7 mm.

Localities.—Brampton Island, holotype; Curtis Island, Port Curtis (J. Laseron).

Remarks.—This is the largest of the species here discussed. The feeble sculpture, well rounded whorls with deep sutures, and the narrowing of the aperture anteriorly are all good characters for recognition. Specimens from Curtis Island are a little smaller than the type, but otherwise conform in all details.

ELODIAMEA MULTICOSTATA, sp. nov.

Fig. 88

Shell of medium size, broad and inflated, with a slightly convex spire, solid, colour a creamy white. Protoconch as in *E. ora*, the nucleus immersed in the summit, followed by a smooth dextral whorl. Mature whorls 4, increasing rapidly, slightly rounded, narrowly stepped at the summits and bent in below to the sutures. Sculpture of numerous, prominent, rounded axial ribs, twisted slightly at the summit of the whorls and rising above the sutures, less than their own width apart, about 25 on the body whorl, fewer on the earlier whorls, continuous to the base where they bend into a shallow umbilical hollow. Aperture extended anteriorly, outer margin nearly flat, anterior margin rounded, inner margin nearly straight, reflected, then bent inwards to make the peristome nearly complete, the single fold very strong and nearly transverse. Length 4·3 mm.

Locality.—1–3 fm Port Curtis (J. Laseron), holotype and one paratype.

Remarks.—Compared with *E. ora*, which it generally resembles, this species is larger and relatively wider, with more flattened whorls which are stepped at the summits, the axial ribs are more numerous and closer together, the columella fold is even stronger, and the peristome is nearly complete.

ELODIAMEA IUGA, sp. nov.

Fig. 89

Shell of medium size, large for the genus, broadly conical, with blunt apex, white. Protoconch probably anastrophic, dome-shaped and smooth, with a small infolded nucleus. Mature whorls 5, of rather irregular growth, rounded, restricted at the sutures, the body whorl inflated. Sculpture of very strong, broad, rounded ribs, less than their own width apart, 14 to the whorl, fading on the base. Aperture extended anteriorly, outer margin thickened, bent in at the suture, nearly straight, anterior margin rounded, broadly reflected, inner margin nearly straight, broadly reflected, with a single very slight, oblique fold, barely visible from in front. Length 5·6 mm.

Locality.—Rocky Island, Cairns (C. Hedley), holotype.

Remarks.—This species resembles *E. caduca* in size, but is narrower, has fewer and more prominent axial ribs, the protoconch is different, and it differs in details of the aperture.

ELODIAMEA PROIECTURA, sp. nov.

Figs. 90 and 91

Shell small, broadly ovate, with convex spire, white. Protoconch anastrophic, small, nearly spherical, at right angles to the main axis. Mature whorls 5, increasing rapidly, nearly flat, narrowly shelved at the summits. Sculpture of strong, rounded axial ribs, close together, about half their own width apart, projecting above the summits of the whorls, about 20 to the whorl, continuous on the base of the body whorl. Aperture extended anteriorly, outer margin nearly straight, anterior and inner margins rounded, the latter reflected, with a single very slight fold, barely visible from in front. Length 3·7 mm.

Locality.—1–3 fm Port Curtis (J. Laseron), holotype.

Remarks.—Though the form and general characters approach such species as *E. kymatodes* the distinct shelf at the summits of the whorls give it a distinct facies. In this last character it resembles *E. multicostata*, but it has fewer axial ribs, and a much weaker columella fold.

ELODIAMEA INVERTA, sp. nov.

Fig. 92

Shell very small, almost cylindrical, white. Protoconch small, anastrophic, almost spherical, partially immersed in summit. Mature whorls 4, with nearly flat sides, broader at the summits, narrowing below to the sutures, making a narrow, rounded shelf, the body whorl relatively long, about half the total length. Sculpture of a few, very large, rounded axial ribs, slightly less than their own width apart, 12 to the whorl, continuous to the base. Aperture extended anteriorly, outer margin nearly flat, anterior and inner margins rounded, the latter narrowly reflected, the single fold very weak, oblique, and barely visible from in front. Length 2·5 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and two paratypes; 15–20 fm off Pt. Charles, Darwin (M. Ward).

Remarks.—The form of this little species is very distinctive with its inverted conical whorls, and the few, very large axial ribs are also distinctive. It cannot readily be compared with any other species here discussed.

Genus EXESILLA, gen. nov.

Type species *Exesilla sulcata*, sp. nov.

Elongated shells with flattened whorls which are more or less medially indented, sculpture of rounded axial ribs which fade on the base, and a weak fold on the inner margin of the aperture which is often invisible from in front.

The form and sculpture are close to *Turbonilla*, but the medially indented whorls make a clear distinction, and the columella fold takes the group closer to such genera as *Elodiamea* in a different subfamily. *Exesilla* constitutes a well-defined group of species in northern Australian waters.

EXESILLA CONICERA, sp. nov.

Fig. 93

Shell small, solid, regularly conical, white. Protoconch small and nearly spherical, half immersed in the summit. Mature whorls 5, increasing regularly, flat, not restricted at the sutures, slightly sinuate below the sutures. Sculpture of low, broad, rounded axial ribs, about their own distance apart, 14–16 to the whorl, fading on the periphery, base of body whorl smooth. Aperture extended anteriorly, outer margin nearly straight and slightly indented, anterior margin rounded, inner margin long, curved, and reflected, with a small oblique fold at its posterior end. Length 2·8 mm.

Locality.—4–14 fm Albany Passage (C. Hedley), holotype and one paratype.

Remarks.—This species is smaller and relatively broader than the others here discussed, otherwise it comes very close to *E. latacosta*.

EXESILLA SULCATA, sp. nov.

Figs. 94 and 95

Shell of medium size, cylindro-conical, solid, elongate, white. Protoconch relatively large, exsert, anastrophic, initial whorls 2, tilted downwards on summit.

Mature whorls 7, flattened, medially sulcate, sutures not deeply impressed. Sculpture of wide, low, rounded axial ribs, close together, about half their own width apart, about 16 to the whorl, fading on the periphery, the base of the body whorl smooth. Aperture extended anteriorly, the outer margin sulcate, anterior margin rounded, inner margin curved and narrowly reflected, with a slight oblique fold, barely visible from in front, a layer of callus on the inside of the body whorl. Length 6 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and numerous paratypes; Lady Elliott Island (C. Hedley); 4–14 fm Albany Passage (C. Hedley).

Remarks.—This is a large and distinctive species, typical of the newly proposed genus.

EXESILLA LATACOSTA, sp. nov.

Figs. 96–99

Shell small, conical, elongate, with a slightly convex spire, white. Protoconch relatively large, anastrophic, prostrate on the summit, of 2 whorls, the second inflated. Mature whorls 7, slightly shouldered, flattened and with a slight medial indentation in the type, other specimens more and others less indented, sutures hardly restricted. Sculpture of strong, rounded axial ribs, rising above the sutures, close together, less than half their own width apart, 20 to the whorl, continuous to, but becoming faint on, the base. Aperture extended anteriorly, outer margin flattened and indented, anterior margin rounded, inner margin curved and narrowly reflected, with a small oblique fold. Length 4 mm.

Localities.—15 fm Palm Islands (C. Hedley), holotype (Fig. 96) and numerous paratypes; 20 fm off Endeavour Reef (A. McCulloch) (Fig. 98); 4–14 fm Albany Passage (C. Hedley) (Fig. 99); 5–10 fm Hope Islands (C. Hedley); Cape Sidmouth (A. U. Henn).

Remarks.—This is a rather variable species, the variation being mainly in the contour of the whorls, the medial indentation almost disappearing in some specimens (Fig. 99). It is very close to *E. sulcata*, but is uniformly smaller, relatively slightly broader, and the axial ribs are broader and more closely packed.

EXESILLA NANA, sp. nov.

Fig. 100

Shell minute, nearly cylindrical, white. Protoconch anastrophic, relatively small, almost spherical. Mature whorls 5, flattened, medially deeply indented, sutures barely impressed. Sculpture of strong, rounded axial ribs, about 18 to the whorl, swollen and almost nodular below the sutures, very close together, fading on the periphery, base of body whorl smooth. Aperture extended anteriorly, outer margin deeply indented, bent in sharply posteriorly and free from the body whorl, making the peristome almost complete, anterior margin rounded, making an obtuse angle with the inner margin, which is slightly curved and narrowly reflected, the faint fold invisible from in front. Length 2·2 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and one paratype; 15 fm Palm Islands (C. Hedley); Cape Sidmouth (A. U. Henn); 4–14 fm Albany Passage (C. Hedley).

Remarks.—This is close in general characters to the two preceding species, but it is much smaller, little more than a third the length of *E. sulcata*, it has fewer whorls, is cylindrical in shape, has a relatively smaller protoconch, and the sculpture is heavier. Specimens from Albany Passage are generally larger than the type and show some variation, some being relatively narrower.

EXESILLA APLINI (Brazier)

Figs. 156 and 157

Turbonilla aplini Brazier, 1877, p. 258.
Turbonilla aplini Brazier. Hedley, 1901, p. 125, pl. 16, fig. 14.

The type is from Katow, New Guinea, and is 8 mm long. Figure 156 is from the type in the Macleay Museum, Sydney University, the protoconch (Fig. 157) is from another specimen from the same locality. Specimens are abundant from 4–14 fm Albany Passage (C. Hedley), and also from 15 fm Palm Islands (C. Hedley).

It is the longest and most attenuate of the species of *Exesilla*, and could easily be mistaken for a species of *Chemnitzia* were it not for the indented whorls and the prominent, almost transverse fold on the inner margin of the aperture.

Genus TATHRELLA, gen. nov.

Type species *Tathrella iredalei*, sp. nov.

Form of shell conical, with rounded whorls, a single columella fold, sculpture of faint axial ribs fading on lower portion of whorls, earlier whorls smooth, and a narrow spiral groove on the periphery.

The type is one of those odd species which will not fit into any recognized group, thus necessitating a new generic name. The axial ribs and lack of spiral sculpture suggest relationship with *Elodiamea*, but the ribs are fainter than in any species of that genus, and the presence of the peripheral groove at once separates it. The type also has the curious, well-exsert anastrophic protoconch associated with the genus *Koloonella*, hereinafter described.

TATHRELLA IREDALEI, sp. nov.

Fig. 101

Shell of medium size, broadly conical, acuminate, white. Protoconch anastrophic, exsert, tilted, sinistral portion planoid. Mature whorls 5, long, well rounded, restricted at the sutures, bending inwards at the summits to form slight rounded shoulders below the sutures, the body whorl long, with a narrow spiral groove on the periphery. Sculpture axial but slight, the early whorls nearly smooth, the penultimate and body whorls with numerous, slight, ill-defined, narrow ribs, which commence below the sutures and fade on the periphery, base of body whorl rounded and smooth. Aperture well extended and narrowed anteriorly, outer and anterior margins rounded, inner margin long and straight, narrowly reflected, with a small posterior oblique fold. Length 5 mm.

Locality.—11 fm Port Curtis (T. Iredale), holotype.

Remarks.—This is a very distinctive species, the characters on which the genus is based at once precluding ready comparison with any other species here discussed.

Genus PAREGILA Laseron

Type species *Odostomia* (*Pyrgulina*) *henni* Brazier.
Paregila Laseron, 1951, p. 312.

Further species from Queensland validate the original generic description. The genus is generally like *Egila* Dall & Bartsch, but the axial ribs stop short above a strong spiral rib on the periphery, the base is excavate, and the single columella fold is strong and transverse, and medially situated on the inner margin of the aperture.

PAREGILA HENNI (Brazier)

Fig. 102

Odostomia (*Pyrgulina*) *henni* Brazier, 1894, p. 171, pl. 14, fig. 2.
Pyrgulina perspectiva Hedley, 1902, p. 10, pl. 3, fig. 33.
Odostomia henni (Brazier). Hedley, 1918, p. 98.

This is the species Hedley described from Cape Sidmouth as *Pyrgulina perspectiva*, but he later (1918) withdrew *perspectiva* as a synonym of *henni*, the type of which came from Port Jackson, New South Wales. The specimen here figured is from 5–8 fm Murray Island (C. Hedley) where it is fairly common. It is 3 mm in length. It is also common in 4–14 fm Albany Passage (C. Hedley), and has also been found in 11 fm Port Curtis (T. Iredale). Comparison with specimens from the type locality show no appreciable difference. This is one of the very few species common to both the Peronian and Solanderian provinces.

PAREGILA ELONGATA, sp. nov.

Fig. 103

Shell of medium size, solid, conical, elongate, with very slightly convex sides, white. Protoconch probably anastrophic, dome-shaped, and smooth, with the small sinistral (?) nucleus immersed in the summit. Mature whorls 6, nearly flat, slightly restricted above the sutures. Sculpture of strong, rounded axial ribs, slightly oblique, about half their own width apart, 18 to the whorl, in the earlier whorls continuous to the sutures, on the body whorl stopping abruptly at the periphery, and separated by a narrow spiral groove from a single, strong, rounded spiral rib. Base of body whorl excavate and smooth. Aperture slightly extended anteriorly, outer and anterior margins rounded, inner margin curved and thickened, with a single, strong, medially situated, transverse fold. Length 4·7 mm.

Locality.—4–14 fm, Albany Passage, holotype.

Remarks.—This is very close in general characters to *P. henni* (Brazier), but is much narrower and more elongate, with an extra whorl, and the axial ribs are fewer and heavier.

Genus BABELLA Dall & Bartsch

Type species *Turbonilla* (*Babella*) *caelatior* Dall & Bartsch (= *caelata* A. Adams).
Babella Dall & Bartsch, 1906, p. 347.

This genus is distinguished from the preceding by the two spiral ribs and the deeply grooved sutures. The type species cited by Dall and Bartsch was *caelatior*

Dall & Bartsch, a new name for *caelata* A. Adams 1864. The latter was originally described as *Parthenia caelata*, but Dall and Bartsch referred it to *Turbonilla*, using *Babella* subgenerically, whereupon it was preoccupied by *Turbonilla caelata* Gould. Since the species is no longer referred to *Turbonilla* s.s. the name *caelata* is no longer preoccupied, hence the specific name becomes *Babella caelata* (A. Adams), with *caelatior* Dall & Bartsch an absolute synonym. The type species comes from Japan, and judging from Dall's and Bartsch's figure, Australian shells are indistinguishable.

Babella caelata (A. Adams)

Figs. 104 and 105

Parthenia caelata A. Adams, 1864, p. 4.
Turbonilla (*Babella*) *caelatior* Dall & Bartsch, 1906, p. 347.

Shell of medium size, solid, conical, spire with straight sides, white. Protoconch anastrophic, prostrate on the summit, of 3 whorls, the third inflated. Mature whorls 6, nearly flat, deeply grooved at the sutures. Sculpture of short, broad, strong, rounded axial ribs, about their own width apart, 18 to the whorl, on the early whorls terminating abruptly well above the sutures, below which is a narrow groove and then a strong spiral rib. On the body whorl there are two strong spiral ribs below the periphery, separated by a deep narrow groove. Base excavate with a swelling immediately adjoining the inner margin of the aperture. Aperture not extended anteriorly, the outer margin indented by the sculpture, anterior margin concave, making a sharp angle with the inner margin, which is long and straight, thickened, and with a single, medially placed, and strong transverse fold. Length 4·8 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), 11 fm Port Curtis (T. Iredale), abundant; 4–14 fm Albany Passage (C. Hedley), abundant; Darwin (J. Laseron), one immature specimen.

Remarks.—This is a distinctive and easily recognized species, the two spiral ribs on the body whorl and the single rib on the early whorls with the deeply grooved sutures making it conspicuous.

Genus EGILA Dall & Bartsch

Type species *Chrysallida lacunata* Carpenter.
Egila Dall & Bartsch, 1904, p. 11.

The main characters taken from the authors' key are: axial ribs extending to the base and crossing a deep peripheral sulcus, the base spirally striate.

A number of Queensland species are doubtfully referred to this genus, as each departs in some characters from the generic description, though conforming in others. The peripheral sulcus differs in depth and may be absent. It may be bounded by two spiral cords, but in *E. univestis* there is only one. Spiral striations are also absent on the bases of all the species, though some species have extra spiral cords which may be enlarged to definite ribs. Most of the species have the general form of *Elodiamea*; all are small and have flattened whorls. A character linking them all is that the whorls are angulated and bent in sharply just above the sutures. Actually, however, few of the species seem closely related, and the only alternative to grouping them together would be to assign each to a separate genus. When further species are discovered their true relationship may become more apparent.

EGILA SPIRALIS, sp. nov.

Fig. 106

Shell very small, broadly conical, with straight sides, white. Protoconch apparently anastrophic, almost spherical and half immersed in the summit. Mature whorls 5, increasing regularly, flat, sharply angled, and bent in to the sutures. Sculpture of numerous narrow, rounded, axial ribs, about their own width apart, about 24 to the whorl, continuous to the base. At the periphery is a deep, rounded, spiral sulcus, which is crossed by the axial ribs, and is bounded above and below by two strong spiral cords, with two more spiral cords on the base. Aperture extended and narrowed anteriorly, outer margin straight, evenly reflected, with an oblique, fairly prominent fold at its posterior extremity. Length 2·8 mm.

Locality.—Darwin (J. Laseron), holotype and one paratype.

Remarks.—Of the northern Australian species this approaches closest to the description of *Egila*, the only difference being that the spiral striations on the base are replaced by the two extra spiral cords.

EGILA TYPICA, sp. nov.

Fig. 107

Shell very small, broadly and regularly conical, spire with straight sides, white. Protoconch apparently anastrophic, nearly spherical, half immersed in the summit. Mature whorls 5, flat, sharply angled and bent in above the sutures. Sculpture of a few, oblique, strong, rounded axial ribs, slightly more than their own width apart, about 12 to the whorl, continuous to but weak on the base. The spiral sulcus below the periphery is pronounced, with strong spiral cords bounding it above and below, but there are neither spiral cords nor striations on the base. Aperture extended and slightly narrowed anteriorly, outer margin straight, anterior margin rounded, inner margin straight and long, evenly reflected, with a fairly strong fold at its posterior extremity. Length 2·7 mm.

Locality.—1–3 fm Port Curtis (J. Laseron), holotype and five paratypes.

Remarks.—Similar in form and size to *E. spiralis*, but with fewer and stronger axial ribs, and without the additional spiral cords on the base.

EGILA ARTICULATA (Hedley)

Fig. 108 (after Hedley)

Odostomia articulata Hedley, 1909, p. 444, pl. 41, figs. 64, 65.

The type locality is 5–10 fm Hope Islands, the length given 3·3 mm. This has not been reidentified, but its distinctive character should make its future recognition easy. The sculpture is of the same type as *E. typica*, but the shell is longer and much narrower, the axial ribs are narrower and more numerous, and there are two more whorls in the adult shell.

EGILA UNIVESTIS, sp. nov.

Fig. 109

Shell small, solid, broadly conical, the spire slightly convex, white. Protoconch probably anastrophic, appearing as a glassy flattened dome on the summit, with the small, sinistral nucleus infolded. Mature whorls 4, flat, sharply angled, and bent in above to the sutures, forming a shelf at the summit of the whorls. Sculpture of strong, rounded axial ribs, about their own width apart, oblique, 16 to the whorl, angled below the periphery, and continuous to the base. The peripheral sulcus is absent, but at the angle of the whorls is a single, strong spiral cord, which is overridden by the axial ribs. In addition, under strong magnification, traces of 2 very fine spiral cords, one above and one below, are also present. Aperture extended anteriorly, outer margin flattened, anterior and inner margins rounded, the latter thickened, the single fold oblique, slight, and at the posterior extremity. Length 2·8 mm.

Locality.—4–14 fm Albany Passage (C. Hedley), holotype and about 20 paratypes.

Remarks.—By the absence of the peripheral sulcus this species does not conform strictly to the definition of *Egila*, but the sharp angulation of the whorls into the sutures and the presence of spiral cords at the angulation gives it the same general facies as the species already discussed, and it is provisionally retained in the same genus.

EGILA CURTISENSIS, sp. nov.

Fig. 110

Shell small, solid, regularly broadly conical, colour dull cream. Protoconch very small, immersed in summit, details not observable, followed by a normal dextral whorl with traces of sculpture. Remaining whorls 5, flattened and even slightly concave, sharply angled below to the sutures, with a broad shelf at the summit of each whorl. Sculpture of strong, rounded axial ribs, oblique, angled where they cross the angulation of the whorls, about their own distance apart, 16 to the whorl, continuous to the base. The spiral sculpture consists of a fairly broad, low rib, linking the axial ribs at the summits of the whorls, and a strong cord crossing the intercostal spaces at the angulation of the whorls, producing a series of rectangular pits. In addition the base is encircled by numerous, fine spiral threads. Aperture extended anteriorly, outer margin flat and sharply angled posteriorly within the aperture, making the peristome almost complete, anterior margin rounded, inner margin rounded and reflected, with a small but distinct oblique fold at its posterior extremity. Length 3·8 mm.

Localities.—11 fm Port Curtis (T. Iredale), holotype and numerous paratypes; 15–20 fm off Pt. Charles, Darwin (M. Ward).

Remarks.—This is a very common species in the type locality. It is close to *E. univestis*, but is more broadly shelved at the summits of the whorls where the axial keels are linked by a spiral rib, it is relatively narrower, and has a whorl more. The characters are constant, though there is a slight variation in size.

EGILA AUSTRALIS, sp. nov.

Figs. 111 and 112

Shell small, conical, elongate and turreted, white. Protoconch anastrophic, recumbent on apex, of 2 whorls, the second inflated. Mature whorls 8, flat, sharply angled, and bent in to the sutures, making a broad shelf at the summits of the whorls. The sculpture consists of strong, rounded, straight axial ribs, about twice their own width apart, about 18 to the whorl, joined at the suture and at the angulation of the whorl by spiral ribs of the same dimension, making on each whorl two series of rectangular pits, the uppermost the largest. On the body whorl the axial ribs terminate abruptly below the periphery at an additional spiral rib, and there is a further smooth spiral rib on the base. Aperture well extended anteriorly, nearly oval, outer margin nearly straight, anterior margin rounded and anteriorly reflected, making an angle with the inner margin which is curved, narrowly reflected, with no apparent fold. Length 4 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and two paratypes; 4–14 fm Albany Passage (C. Hedley), a number of specimens.

Remarks.—This is a very distinctive species which cannot readily be compared with any other Australian species here discussed. It is very doubtfully referred to *Egila*, but by the sharp angulation of the whorls into the sutures, and by its sculpture it seems the extreme development of the other species here referred to that genus. It is in fact much closer to the west American species *Ividella pedroana* Dall & Bartsch, but that again is an extreme species which fits less with other species of *Ividella* Dall & Bartsch than it does with their own *Egila*.

Genus EURATHEA, gen. nov.

Type species *Eurathea humerica*, sp. nov.

A small shell from Darwin will not fit in any genus hitherto proposed, and necessitates the proposal of a new generic name for its reception. The main generic character is a strong sulcus immediately below the suture, below which the whorl is angulate, producing a strong shoulder. The sculpture consists of axial ribs which cross the sulcus and fade on the base, which is encircled by fine spiral cords.

The characters broadly resemble *Egila*, but the sulcus is on the shoulder of the whorl and not the periphery, giving the whole a very different facies.

EURATHEA HUMERICA, sp. nov.

Fig. 113

Shell small, solid, broadly conical, white. Protoconch minute, embedded in the summit, details not observable, the first dextral whorl with faint sculpture. Mature whorls 5, long, increasing rapidly and regularly, slightly rounded and sloping in below to the sutures, with a rounded sulcus below the sutures, below which is a pronounced shoulder. Sculpture of narrow axial ribs, well apart, about 16 to the whorl, crossing the sulcus and fading on the periphery of the body whorl. Base of body whorl rounded, encircled by fine spiral cords, which in the type are difficult to detect. Aperture slightly extended anteriorly, oval, all the margins rounded and thickened, the outer margin posteriorly indented by the sulcus, the inner margin with a very slight oblique fold, invisible from in front. Length 3·2 mm.

Locality.—Darwin (J. Laseron), holotype.

Remarks.—This so far unique species is so distinctive that there is no other with which it can readily be compared.

Genus PYRGULINA A. Adams

Type species *Chrysallida casta* A. Adams, 1864, p. 4.

The characters given for *Pyrgulina* are "strong axial ribs which extend to the umbilical area; intercostal spaces marked by fine incised spiral lines".

In New Zealand, Laws (1941) discriminated between those species in which the intercostal spaces are crossed by fine incised lines and those with the spaces crossed by raised spiral threads. He separated the latter from *Pyrgulina*, proposing the new genus *Linopyrga*. Laseron (1951) used both genera for a number of Peronian species.

In northern Australia is a group of small species very like *Elodiamea* in form, but with fine intercostal spiral sculpture which is often hard to detect, though it appears to be that of *Pyrgulina*. This genus is therefore used for them. On the other hand, other species, generally larger and more elongate, definitely have the spiral sculpture of *Linopyrga*, and they are placed there.

PYRGULINA OODES (Watson)

Fig. 114

Odostomia oodes Watson, 1886, p. 485, pl. 31, fig. 6.

The type locality is 7 fm Flinders Passage, Cape York, the length given 0·064 in. (1·6 mm). A number of specimens were sorted from material collected by the late C. Hedley from 4–14 fm Albany Passage, and one is here figured which is 2 mm in length. They are a little larger than the type, but otherwise agree in detail with Watson's description and figure. A characteristic is the sharp bending of the outer margin posteriorly into the aperture, making the peristome almost complete.

PYRGULINA SPISSA, sp. nov.

Figs. 115 and 116

Shell small, solid, broadly conical with a slightly convex spire, white. Protoconch dome-shaped, with a small, probably anastrophic nucleus immersed in the summit. Mature whorls 4, increasing regularly, slightly rounded, slightly restricted at the sutures. Sculpture of numerous, strong, rounded axial ribs, a little less than their own width apart, about 20 to the whorl, persistent to the base; spiral sculpture very fine and difficult to detect, consisting apparently of fine incised lines in the intercostal spaces. Aperture extended anteriorly, outer margin rounded and posteriorly thickened, anterior margin rounded, inner margin rounded and reflected, with a single, distinct, oblique fold at the posterior end. Length 3 mm.

Localities.—4–14 fm Albany Passage (C. Hedley), holotype (Fig. 115) and numerous paratypes; Darwin (J. Laseron), fairly common; 5–10 fm Hope Islands (C. Hedley); 20 fm off Endeavour Reef (A. McCulloch); 11 fm Port Curtis (T. Iredale), common.

Remarks.—Compared with *P. oodes* (Watson) this species is uniformly larger, has one more whorl, is conical instead of ovate in form, and differs in details of the aperture. The Darwin specimens differ slightly by having fewer and larger ribs which fade on the base, but otherwise conform. They may possibly constitute a distinct race, but the difference is hardly specific. One is here figured (Fig. 116) for comparison. It is 3 mm in length.

PYRGULINA AFFINIS, sp. nov.

Fig. 117

Shell small, solid, conical, spire slightly convex, white, and translucent. Protoconch large, smooth, and dome-shaped with the minute, possibly anastrophic nucleus immersed in the summit. Mature whorls 5, slightly rounded, restricted at the sutures, relatively long, increasing regularly. Sculpture of strong, rounded axial ribs, slightly less than their own width apart, about 24 to the whorl, persistent to the base. The spiral sculpture is again faint and difficult to detect, consisting of very fine lines in the intercostal spaces. Aperture extended anteriorly, outer and anterior margins rounded, inner margin rounded and narrowly reflected, the single fold oblique and barely visible from in front. Length 4 mm.

Localities.—Darwin (J. Laseron), holotype and nine paratypes; Port Moresby, New Guinea (C. Hedley), abundant; 1–3 fm Port Curtis (J. Laseron).

Remarks.—The single Port Curtis specimen is 4·6 mm in length, rather larger than the type, and some of the Port Moresby specimens are also a little larger. Compared with *P. spissa*, to which it is probably closely related, this species is uniformly larger and narrower, it has an extra whorl, and the body whorl is shorter in relation to the total length. The axial ribs are also more numerous. Including *P. oodes*, when mixed together, the three species can be readily initially sorted by their respective lengths, *P. oodes* being close to 2 mm, *P. spissa* to 3 mm, and *P. affinis* to 4 mm.

Genus LINOPYRGA Laws

Type species *Odostomia rugata* Hutton.
Linopyrga Laws, 1941, p. 7.

As stated in the discussion on *Pyrgulina*, that genus differs from *Linopyrga* by having the spiral intercostal sculpture as incised lines, whereas in *Linopyrga* it is in the form of raised threads. Laws also remarks that the New Zealand species he assigned to his genus have a subsutural swelling. It is doubtful if this last character has generic significance, but if so it would separate the Australian species assigned to *Linopyrga*, for none of them shows it. Of the Australian species, also, most are generally larger than species of *Pyrgulina*; they are more elongate, the spiral sculpture is more easily detected, and the axial ribs are often narrower and farther apart.

LINOPYRGA MACCULLOCHI (Hedley)

Fig. 118 (after Hedley)

The type locality is 5–10 fm Hope Islands, the length 4·5 mm. This species has not since been reidentified, but its ovate form, long whorls, narrow axial ribs which project above the sutures and fade on the base, and its strong columella fold should facilitate its future recognition.

LINOPYRGA DELICATULA, sp. nov.

Fig. 119

Shell of medium size, elongate and conical, white. Protoconch of a single, inflated, smooth glassy whorl, with the anastrophic apex partially immersed in the summit. Mature whorls 7, long, rounded, restricted at the sutures and slightly shouldered at the summits. Sculpture of narrow, raised, rounded axial ribs, nearly twice their own width apart, 14 to the whorl, continuous to the base. Spiral sculpture of fine raised threads, very close together, crossing the broad, nearly flat intercostal spaces. Aperture slightly extended anteriorly, outer and anterior margins rounded, inner margin curved, very narrowly reflected, the single fold very slight, oblique, hardly visible from in front. Length 7 mm.

Localities.—Hervey Bay (J. Laseron), holotype; Peel Island, Moreton Bay (Mrs. J. Kerslake).

Remarks.—This is a very distinctive species, the slender elongate form, long whorls, and narrow, distant axial ribs distinguishing it from all the other species here discussed.

LINOPYRGA OREADES, sp. nov.

Fig. 120

Shell of medium size, elongate, conical, spire very slightly convex, colour yellowish, fading to white. Protoconch a single dextral, smooth, inflated whorl, the nucleus immersed in its summit, its anastrophic character obscured. Mature whorls 6, rounded, restricted at the sutures. Sculpture of strong, broad, rounded axial ribs, less than their own width apart, 12 to the whorl, continuous to the base. Spiral sculpture of fine, raised threads crossing the intercostal spaces. Aperture extended anteriorly, outer and anterior margins rounded, inner margin curved and narrowly reflected, the single fold faint and invisible from in front. Length 6 mm.

Localities.—Cairns (C. Hedley), holotype and seven paratypes; 1–3 fm Port Curtis (J. Laseron), common.

LINOPYRGA DECLIVITA, sp. nov.

Fig. 121

Shell of medium size, regularly conical, elongate, white. Protoconch as in *L. oreades*, a single, smooth, inflated dextral whorl, with the probably anastrophic apex immersed in the summit. Mature whorls 7, nearly flat and not restricted at the sutures. Sculpture of raised axial ribs, about their own width apart, very oblique, 16–18 to the whorl, continuous to the base. The spiral sculpture is of numerous, fine, raised threads crossing the intercostal spaces. Aperture as in *L. oreades*, extended anteriorly, the outer, anterior, and inner margins rounded, the last narrowly reflected, the single fold faint and not visible from in front. Length 5·5 mm.

Locality.—Cairns (C. Hedley), holotype and seven paratypes.

Remarks.—This species is very close to *L. oreades*, and indeed in the original sorting the two were mixed together as one species. Close examination showed, however, that there were two forms, each constant and easily separable from each other. The main differences are that *L. declivita* has much flatter whorls, the ribs are oblique, narrower, and more numerous.

LINOPYRGA sp.

Fig. 122

Two specimens from 15 fm off Palm Islands (C. Hedley) are close in general characters to *L. declivita*, but they are larger, the lower part of the spire tends to become cylindrical, and though the axial ribs approximate in number and size they are perfectly straight and not oblique. More and better material is necessary to decide if this is still another species. One specimen, 6·5 mm in length without the protoconch, is here figured for future reference.

LINOPYRGA INCURVA, sp. nov.

Fig. 123

Shell very large for the genus, elongate, regularly conical, white. Protoconch a broad, smooth dome, with the apex, probably anastrophic, immersed in the summit. Mature whorls 8, relatively short, nearly flat, and medially slightly indented, sutures not impressed. Sculpture of strong, broad, rounded axial ribs, very close together, straight, continuous to the base. Spiral sculpture of numerous, fine, raised threads crossing the intercostal spaces. Aperture extended anteriorly, outer margin flattened, anterior margin broken in the type, inner margin short, straight, greatly thickened, producing a wide column, with a single, strong, nearly transverse fold, posteriorly situated. Length 10 mm.

Locality.—Brampton Island, holotype.

Remarks.—The large size, flat, medially indented whorls, and the characters of the aperture separate this from all other species here discussed.

LINOPYRGA PERSCALATA (Hedley)

Fig. 124

Turbonilla perscalata Hedley, 1909, p. 449, pl. 42, fig. 75.

The type locality is 5–10 fm Hope Islands, the length of the type 2·2 mm. Hedley placed this species in *Turbonilla*, but it is hard to see any relationship with that or any allied genera. Hedley's figure also shows a slight fold on the inner margin of the aperture, and the specimens here identified as *perscalata* also show this fold, though in many it is invisible from in front. The specimen here figured is from Caloundra, and is 2·3 mm in length. It matches the type well, though relatively a little broader, but Hedley states that in the type locality specimens vary both in size and width. Other specimens examined are from 1–3 fm Port Curtis (J. Laseron); Bowen (J. Laseron); 5–8 fm Murray Island (C. Hedley); and Darwin (J. Laseron), showing that the species has a wide range.

LINOPYRGA RETICULATA, sp. nov.

Fig. 125

Shell small, broadly conical, colour pale cream. Protoconch anastrophic, relatively large, almost spherical, half immersed in summit. Mature whorls 4, with nearly straight sides, broadly stepped at the summits, whorls individually cylindrical, body whorl relatively long, about half the total length. Sculpture of raised, narrow axial ribs, well separated, 18 to the whorl, continuous to the base. Spiral sculpture of distant, well-defined spiral cords, about 5 to the whorl, about 7 on the body whorl, crossing the intercostal spaces, which are flat, making a series of nearly square, shallow pits, and giving the whole a reticulate appearance. Aperture well extended anteriorly, narrowed anteriorly, outer margin straight, inner margin curved, very narrowly reflected, the single oblique fold barely visible from in front. Length 2·8 mm.

Locality.—11 fm Port Curtis (T. Iredale), holotype and one paratype.

Remarks.—This is a very distinctive species, the widely shouldered whorls and regular reticulated sculpture distinguishing it from all other species here discussed. The sculpture brings it within *Linopyrga*, but the general facies suggests it may have other relationship.

Genus QUIRELLA, gen. nov.

Type species *Quirella mirationis*, sp. nov.

Quirella is proposed for minute, broad shells with few whorls and greatly enlarged body whorls, with sculpture like *Linopyrga*, except that the spiral sculpture is not confined to the intercostal spaces, but overrides the axial ribs.

QUIRELLA MIRATIONIS, sp. nov.

Fig. 126

Shell minute, broadly ovate, white. Protoconch probably anastrophic, but minute and immersed in the summit. Mature whorls 3, increasing rapidly, the body whorl very large and inflated, the margins slightly rounded, broadly stepped at the summits. Sculpture of numerous, narrow, rounded, raised axial ribs, more than their own width apart, about 22 to the whorl, curving over the stepped summits of the whorls to the sutures, and continuous to the base, bending in to a shallow umbilical hollow. The spiral sculpture consists of numerous fine threads which cross the intercostal spaces and override the axial ribs. Aperture of type slightly imperfect, but not extended anteriorly, outer and anterior margins rounded, inner margin curved and reflected, the slight fold invisible from in front. Length 2·2 mm.

Locality.—Bowen (J. Laseron), holotype and two immature specimens.

Remarks.—By its form this minute species obviously needs a new generic as well as specific name, and the spiral threads overriding the axial ribs also separate it from any species of *Linopyrga*, the genus it most closely resembles.

QUIRELLA SUPRAFILA, sp. nov.

Fig. 127

Shell minute, broadly conical, white. Protoconch with a minute anastrophic apex, partially immersed in the summit, followed by a smooth dextral whorl, normal with the main spire. Remaining whorls 3, stepped at the summits, flattened and even slightly indented, the body whorl large. Sculpture of narrow, distant, axial ribs, 14–16 to the whorl, continuous to the base. The spiral sculpture consists of fine, close, raised threads, which cross the flat intercostal spaces and override the axial ribs. Aperture extended anteriorly, the outer margin flat and thickened, the anterior and inner margins widely reflected, the fold very slight and invisible from in front. Length 2·7 mm.

Localities.—Murray Island, holotype; 4–14 fm Albany Passage (C. Hedley); Darwin (J. Laseron).

Remarks.—This species generally resembles *Linopyrga perscalata* (Hedley), but can be readily separated by its greater width, flattened instead of rounded whorls, and more importantly by the spiral threads overriding the axial ribs, though the last character can only be detected under considerable magnification. Compared with *Q. mirationis* it is narrower, has a different contour, and the axial ribs are fewer and farther apart.

Genus MIRALDA A. Adams

Type species *Parathenia diadema* A. Adams.
Miralda A. Adams, 1864, p. 3.

The type species came from Japan, and the genus seems a natural one, with many species distributed through the tropical waters of the western Pacific. The species are typically minute, with short, ovate shells of not more than 4 whorls, the sculpture of strong spiral ribs, which are crossed near the summits of the whorls by short axial ribs, making this portion sometimes cancellate or tuberculate. The axial sculpture seldom persists past the first three spiral ribs from the summit of the whorl, but in one species with otherwise the general facies of the genus, it persists to the base, and makes the whole sculpture cancellate. The protoconchs are markedly anastrophic, and the single columella fold is generally prominent, but is weak in some species.

MIRALDA SENEX (Hedley)

Figs. 128 (after Hedley) and 129

Pyrgulina senex Hedley, 1902, p. 10, pl. 3, fig. 31.

The type locality is 13 fm, 10 miles south of Cape Sidmouth, the length of the type given 1·57 mm. Though somewhat variable it is easily recognized, and material is available from several localities, including 8–10 fm Hope Islands (C. Hedley); 4–14 fm Albany Passage (C. Hedley); and 1–3 fm Port Curtis (J. Laseron). From a long series from Hope Islands the variation is seen to be in the form, as some specimens are more cylindrical than others, in the number of spiral ribs on the base, and in the degree to which the short axial ribs make the upper portion of the whorls tuberculate. A specimen from Curtis Island 2·2 mm in length shows about the extreme in variation and is here figured (Fig. 129) for comparison with a copy of Hedley's original figure (Fig. 128).

MIRALDA UMERALIS (Hedley)

Fig. 130 (after Hedley)

Pyrgulina umeralis Hedley, 1902, p. 11, pl. 3, fig. 32.

The type locality is 13 fm Princess Charlotte Bay, the length given 1·72 mm. It has not yet been reidentified, but Hedley's figure and description show it to be very close to *M. senex*, the main difference being in form, *umeralis* being more conical and narrowed at the apex. Hedley was evidently satisfied that the two species are distinct, as they were both proposed in the same paper and figured side by side.

MIRALDA CONICA, sp. nov.

Fig. 131

Shell small, broadly and regularly conical, with an acute apex, greyish white. Protoconch small, anastrophic, nearly spherical, half immersed in about half the summit. Mature whorls 4, increasing regularly, flat, sutures a deep U-shaped channel. Sculpture primarily of strong, rounded spiral ribs separated by smooth rounded channels, 3 on the early whorls and 7 on the body whorl, becoming smaller on the rounded base. The axial sculpture consists of short, rather narrow axial ribs, varying from 14–18 to the whorl, crossing the two upper spiral ribs and rising above them as rounded tubercles. Aperture extended anteriorly, outer margin rounded and indented by the spiral ribs, anterior margin rounded, inner margin curved and reflected, with a single, small oblique fold, barely visible from in front. Length 3 mm.

Locality.—11 fm Port Curtis (T. Iredale), holotype and six paratypes.

Remarks.—This is larger than the two previous species, and differs in form, being regularly conical with an acute apex. It is closer to *M. umeralis* than to *senex*, but is also relatively narrower, and has an extra whorl.

MIRALDA RUGOSA, sp. nov.

Fig. 132

Shell minute, solid, broadly ovate with a convex spire, white. Protoconch anastrophic, the sinistral apex half immersed in the summit, followed by a smooth, normal dextral whorl. Mature whorls 3, flattened, increasing regularly, stepped at the summits, sutures deep and channelled. Sculpture of both strong spiral and axial ribs, the spiral ribs 3 on the early whorls, 7 on the body whorl. The axial ribs number 14 to the whorl, and are more persistent than on the previous species, overriding the spiral ribs and rising above them in rounded gemmules, producing a deep cancellation, but becoming weaker on the base, where the cancellation is not so marked. Aperture not produced anteriorly, outer margin indented by the sculpture, lirate within, anterior margin rounded, inner margin curved, narrowly reflected, with a single, fairly strong, oblique fold at the posterior extremity. Length 2·3 mm.

Localities.—5–10 fm Hope Islands (C. Hedley), holotype and 14 paratypes; 11 fm Port Curtis (T. Iredale).

Remarks.—In form and general characters this is a typical *Miralda*, though the persistence of the axial ribs distinguishes it from other species. From *M. senex*, with which it was associated in the type locality, it was readily separated by its cancellate sculpture. The Port Curtis specimens are a little larger than the type, but otherwise conform in all details.

MIRALDA REVINCTA (Hedley)

Fig. 133 (after Hedley)

Odostomia revincta Hedley, 1912, p. 144, pl. 42, fig. 25.

The type locality is 15 fm off Palm Islands, the length given 1·35 mm. This minute species has not been reidentified, but the single row of large gemmules below the suture should make its future recognition certain.

MIRALDA ZEA (Hedley)

Fig. 134

Pyrgulina zea Hedley, 1902, p. 11, pl. 3, fig. 34.

The type locality is 13 fm, 10 miles south of Cape Sidmouth, the length given 1·8 mm. The specimen here figured is from 4–14 fm Albany Passage (C. Hedley), and is rather larger, having a length of 2·6 mm. Otherwise it agrees very well with Hedley's description and figure, being more conical in shape that *M. senex*, and with the axial ribs crossing three of the spiral ribs instead of two. These three spiral ribs are also broken into large round gemmules, and the sculpture of the upper part of the body whorl is strongly cancellate.

MIRALDA COLUMNA, sp. nov.

Fig. 135

Shell minute, nearly cylindrical, with a flattened apex, white. Protoconch minute, nearly entirely immersed in the summit, details unobservable. Mature whorls 4, the first short, remainder long, slightly rounded, narrowly stepped at the sutures. Sculpture finely reticulate, the axial ribs narrow, more than their own width apart, about 18 to the whorl, persistent nearly to the base. The spiral sculpture is of strong cords, rather weaker than the axial ribs, about 10 on the body whorl, crossing the intercostal spaces but not overriding the axial ribs. Aperture extended anteriorly, outer and anterior margins thin and rounded, inner margin rounded, narrowly reflected, with a single slight oblique fold. Length 2 mm.

Locality.—15 fm Palm Islands (C. Hedley), holotype and two paratypes.

Remarks.—This species is doubtfully referred to *Miralda*, as the sculpture suggests *Linopyrga*, except that in no species of *Linopyrga* studied is the spiral sculpture so strong. The general form is, however, similar to *Miralda*, of which, for the present, it can be considered the extreme development.

MIRALDA TRIBULATIONIS (Hedley)

Fig. 136 (after Hedley)

Odostomia tribulationis Hedley, 1909, p. 448, pl. 41, fig. 72.

The type locality is 5–10 fm Hope Islands, the length of the type 1·65 mm. Hedley also records it from the Palm Islands and Masthead Island. It is now again recognized from 4–14 fm Albany Passage, and specimens are so close to the type that Hedley's figure might well be the drawing of one of them, except that the largest is 2·3 mm in length. The well defined axial ribs on the upper portion of the whorls, the fine spiral ribs on the base, and the regularly ovate form are distinctive characters.

MIRALDA sp.

Fig. 137

A single specimen from 11 fm Port Curtis (T. Iredale) is very close to *M. tribulationis*, but more material is needed to decide if it is a distinct species. It is slightly larger, 2·5 mm in length, has a slightly different form, the axial ribs are oblique, and there is no spiral sculpture discernible between the axial ribs on the upper portion of the whorls. It is here figured for future reference.

Subfamily **TURBONILLINAE**

Genus TURBONILLA Risso

Type species *Turbonilla plicatula* Risso.
Turbonilla Risso, 1826, p. 224.

Elongate, many-whorled shells, with prostrate anastrophic protoconchs, the inner margin of the aperture reflected, but without any fold, whorls rounded, sculpture of well-defined axial ribs which are continuous to or fade on the base, spiral sculpture absent.

Dall and Bartsch (1904, p. 4) wrongfully changed the name of the type species to *typica* on the grounds of *plicatula* having been preoccupied by *Turbo plicatulus* Scacchi. As this is quite a different shell described under a different generic name, *plicatula* Risso must be restored.

TURBONILLA TENUISSIMA Hedley

Fig. 138

Turbonilla tenuissima Hedley, 1909, p. 450, pl. 42, fig. 78.

This is a minute shell, the type of which came from the Hope Islands and is only 2·3 mm in length. Two specimens from the Prince of Wales Island are here identified with a little uncertainty because, although they conform in most details, they are a little larger, the one figured being 3 mm in length. Hedley also states that the first two or three whorls of the type are smooth, whereas in those from the Prince of Wales Island the early whorls are faintly sculptured. But the slightest wear could obscure this character, and it is felt that separation on these grounds would not be justified.

TURBONILLA DARWINENSIS, sp. nov.

Figs. 139 and 140

Shell very small, slender, nearly cylindrical, white, vitreous, and translucent. Protoconch relatively large, anastrophic, prostrate on summit, a small nucleus, the second whorl inflated. Mature whorls 5, relatively long, evenly rounded, restricted at the sutures. Sculpture of thin, straight axial ribs, about their own width apart, about 20 to the whorl, continuous to but becoming faint on the base, the lower part of the base with very fine spiral threads. Aperture ovate, extended anteriorly, outer and anterior margins thin and rounded, inner margin nearly straight and very narrowly reflected. Length 3 mm.

Locality.—Darwin (J. Laseron), holotype and one paratype.

Remarks.—This is a delicate little species, in some characters resembling *T. tenuissima*, but more cylindrical in form, with longer whorls and a larger protoconch. The faint spiral threads on the base are hardly in accordance with *Turbonilla*, but the character is so slight that it hardly justifies generic separation.

TURBONILLA BOWENENSIS, sp. nov.

Figs. 141 and 142

Shell of medium size, elongate, slender, conical, becoming cylindrical in the lower portion of the spire, thin, white, and translucent. Protoconch wider than summit of shell, anastrophic, prostrate on summit, nucleus relatively large, followed by an inflated whorl. Mature whorls 9, well rounded, restricted at the sutures, body whorl short. Sculpture of narrow, rounded axial ribs, less than their own width apart, about 28 to the whorl, continuous on the base. Aperture small, short, only slightly extended anteriorly, outer and anterior margins rounded, the latter making an angle with the inner margin, which is straight and narrowly reflected. Length 6·5 mm.

Locality.—Bowen (J. Laseron), holotype and two paratypes.

Remarks.—This is a delicate species, more than twice the size of the two preceding species, from which it also differs by the more rounded whorls, the more numerous axial ribs, and the straight inner margin of the aperture.

TURBONILLA NINONA, sp. nov.

Fig. 143

Shell of medium size, nearly cylindrical in lower portion of spire, early portion conical, elongate, slender, white, and opaque. Protoconch anastrophic, prostrate on summit, of medium size, with 2 whorls, the nucleus relatively large, the second whorl inflated. Mature whorls 11, short, slightly rounded, and restricted at the sutures, body whorl of type slightly swollen. Sculpture of narrow, raised, rounded axial ribs, about their own width apart, about 22 to the whorl, continuous on the base. Aperture slightly extended anteriorly, the outer, anterior, and inner margins continuously rounded, the last narrowly reflected. Length 7·5 mm.

Locality.— 4–14 fm Albany Passage (C. Hedley), holotype and one paratype.

Remarks.—This species resembles *T. bowenensis*, but the whorls are relatively shorter and less rounded, and the axial ribs are fewer.

TURBONILLA VITREA, sp. nov.

Fig. 144

Shell of medium size, elongate, slender, regularly conical, white, vitreous, and translucent. Protoconch relatively large, wider than the summit, anastrophic, at right angles to the main axis, flattened, and nearly discoidal. Mature whorls 9, slightly rounded, very slightly restricted at the sutures. Sculpture of broad, low, rounded axial ribs, about their own width apart, 14 to the whorl, fading just below the periphery, leaving the base of the body whorl smooth. Aperture extended anteriorly, the outer and anterior margins rounded, inner margin nearly straight and narrowly reflected. Length 5·2 mm.

Localities.—4–14 fm Albany Passage (C. Hedley), holotype and 18 paratypes; Darwin (J. Laseron), common.

Remarks.—Compared with the several previous species this has a slightly different contour, is a little broader, and has fewer and broader axial ribs. It can be readily picked out by the very vitreous texture and shining surface. It is nearly constant in its characters, though there is a slight variability in size and relative width.

TURBONILLA CORRIGEA, sp. nov.

Figs. 145 and 146

Shell relatively large and robust, elongate, lower portion of spire nearly cylindrical, upper portion conical, white, and polished. Protoconch small, anastrophic, obliquely overhanging on summit, flattened, and almost disk-like. Mature whorls 11, short, very slightly rounded, and hardly restricted at the sutures. Sculpture of broad, rather irregular axial ribs, narrowed and slightly flattened at their summits, about their own width apart, about 20 to the whorl, intercostal channels rounded, fading just below the periphery, base of body whorl smooth. Aperture slightly extended anteriorly, outer and anterior margins rounded, inner margin straight and reflected. Length 9·4 mm.

Locality.—Darwin (J. Laseron), holotype and two paratypes.

Remarks.—This is nearest to *T. vitrea* of the species here described, but it is a larger, more robust species, with shorter whorls and more numerous axial ribs. The nearly flattened summits of the axial ribs form reflecting surfaces to light and give the species a distinct facies.

TURBONILLA PAUCINA, sp. nov.

Fig. 147

Shell of medium size, elongate and narrow, lower portion of spire cylindrical, the last three whorls nearly equal, upper portion conical and slightly convex, white. Protoconch rather wider than the summit, anastrophic, at right angles to the main axis, nearly spherical. Mature whorls 8, long, slightly shelved at the summits, nearly flat, with the taper slightly reversed. Sculpture of broad, rounded axial ribs, more than their own width apart, 12 to the whorl, becoming slightly nodular above and fading on the base. Aperture extended anteriorly, outer and anterior margins rounded, inner margin curved and narrowly reflected. Length 5 mm.

Locality.—Port Curtis (J. Laseron), holotype and ten paratypes.

Remarks.—The form, long whorls, and the few, widely separated axial ribs make this a distinctive and easily recognizable species.

TURBONILLA CONICA, sp. nov.

Figs. 148 and 149

Shell small, regularly conical, with a relatively broad base and rapid taper, elongate, white. Protoconch relatively large and well exsert, anastrophic, almost spherical, tilted downwards to main axis of shell. Mature whorls 8, increasing regularly, flat and very slightly indented medially, not restricted at the sutures, body whorl short, curving in sharply at the base. Sculpture of broad, low, rounded axial ribs, more than their own width apart, 14 to the whorl, fading at the periphery, base smooth. Aperture extended anteriorly, outer margin flat and indented, anterior margin rounded, inner margin curved, reflected, slightly swollen at the posterior extremity suggesting a fold. Length 4·7 mm.

Localities.—20 fm off Endeavour Reef (A. McCulloch), holotype and three paratypes; Cape Sidmouth (A. U. Henn); 15 fm Palm Islands (C. Hedley).

Remarks.—The regularly conical form, with narrow apex and relatively broad base, make this species easy to recognize. The flat, slightly indented sides of the whorls and the suggestion of a columella fold raise doubts of its generic position, and suggest a relationship with *Exesilla*, described earlier in this paper.

TURBONILLA MICROSCOPICA, sp. nov.

Figs. 150 and 151

Shell minute, broadly ovate-conical, with convex spire, white. and translucent. Protoconch relatively large, anastrophic, prostrate on summit, of 2 whorls, the second inflated. Mature whorls 5, rounded, restricted at the sutures. Sculpture of narrow axial ribs, more than their own width apart, 16 to the whorl, continuous to the base. Spiral sculpture is visible under high magnification as minute striations on the sides of the axial ribs and in the intercostal grooves. Aperture not extended anteriorly, outer and anterior margins rounded, inner margin curved and narrowly reflected. Length 2 mm.

Locality.—Darwin (J. Laseron), holotype and seven paratypes.

Remarks.—Again this is doubtfully referred to *Turbonilla*; it is smaller, broader, and has fewer whorls than any species of *Turbonilla* here discussed, and but for the absence of a columella fold approximates in form and sculpture to *Pyrgulina* in a different subfamily.

TURBONILLA FELICITA, sp. nov.

Figs. 152 and 153

Shell of medium size, elongate and attenuate, white. Protoconch anastrophic, almost spherical, tilted downwards on summit. Mature whorls 11, relatively long, slightly rounded, and restricted at the sutures. Sculpture of broad, low, rounded axial ribs, less than their own width apart, 18 on the later whorls, fewer on the earlier whorls, fading on the base. Aperture extended anteriorly, outer and anterior margins rounded, inner margin curved and widely reflected. Length 6·3 mm.

Locality.—15–20 fm off Pt. Charles, Darwin (M. Ward), holotype and one paratype.

Remarks.—This is the slenderest of all the species of *Turbonilla* here discussed. From the slender species of *Chemnitzia*, and apart from its typical *Turbonilla* sculpture, it can be distinguished by its longer whorls.

Genus CHEMNITZIA d'Orbigny

Type species designated by Dall and Bartsch *Melania campanellae* Philippi.
Chemnitzia d'Orbigny, 1839, p. 77.

Like *Turbonilla* without spiral sculpture, but the axial ribs stop abruptly at the periphery, and the intercostal furrows are deeply excavated below the general level of the surface, ceasing in line with the terminations of the axial ribs. The axial ribs are generally oblique, and many species are exceedingly attenuate.

CHEMNITZIA DARNLEYENSIS (Brazier)

Figs. 154 and 155

Turbonilla darnleyensis Brazier, 1877, p. 257.
Turbonilla darnleyensis Brazier. Hedley, 1901, p. 124, pl. 16. fig. 12.

The Figures are drawn from the holotype which is in the Macleay Museum, Sydney University, and came from Darnley Island; its length is 7 mm. It is abundant in 4–14 fm Albany Passage (C. Hedley); also at 1–3 fm Port Curtis (J. Laseron); and at Darwin (J. Laseron). When Hedley revised the types of the *Chevert* Expedition he synonymized *Turbonilla dipsycha* Watson under *darnleyensis*, but reference to Watson's description and figure shows that *dipsycha* is a much smaller species with spiral sculpture, and it is here restored under the generic name *Pyrgiscilla.*

C. darnleyensis is a well-defined and common species with a wide distribution. It is a typical *Chemnitzia*, and among other characters can be mentioned the three-whorled, prostrate, anastrophic protoconch, projecting beyond the summit, and present in many of the species.

CHEMNITZIA GABRIELI (Hedley)

Figs. 158 and 159*

Turbonilla gabrieli Hedley, 1909, p. 449, pl. 52, fig. 74.

The type came from 5–10 fm Hope Islands. The specimen figured is from 1–3 fm Port Curtis (J. Laseron), and is 6 mm in length, rather larger than the type which may not be quite mature. It is a widespread species, both on the Queensland coast and the Barrier Reef, and specimens have been examined from 4–14 fm Albany Passage (C. Hedley), and Darwin (J. Laseron). It is the slenderest and most attenuate of the Queensland species, and is slightly variable: some specimens, notably from Darwin, are so attenuate that the spire has practically no taper at all.

*For description of Figures 156 and 157, see *Exesilla aplini* (Brazier) after Figure 100.

CHEMNITZIA PORRECTA, sp. nov.

Figs. 160 and 161

Shell relatively large, slender, elongate, tapering to an acute apex, white, shining, and translucent. Protoconch relatively large and exsert, anastrophic, prostrate on summit, of 2 whorls, the second swollen. Mature whorls 16, short, slightly rounded and restricted at the sutures. Sculpture of strong, rounded, oblique axial ribs, about their own width apart, 18 to the whorl, stopping abruptly at the periphery. Intercostal grooves deeply excavated, below the general level of the surface of the shell, also stopping abruptly on the periphery in line with the termination of the axial ribs, base of body whorl smooth and rounded. Aperture well extended anteriorly, outer and anterior margins rounded, the latter making a sharp angle with the inner margin, which is straight and narrowly reflected. Length 9·5 mm.

Localities.—Bowen (J. Laseron), holotype and six paratypes; 5–10 fm Hope Islands (C. Hedley); 20 fm off Endeavour Reef (A. McCulloch); 4–14 fm Albany Passage (C. Hedley); Darwin (J. Laseron), very abundant.

Remarks.—Like *C. gabrieli* this is a common and widespread species, and shows little variation throughout its range. Compared with *gabrieli* it is on the whole larger, is not quite so slender, tapers more rapidly, and the axial ribs are more numerous.

CHEMNITZIA QUEENSLANDICA, sp. nov.

Figs. 162 and 163

Shell relatively large, elongate, tapering to an acute apex, white, shining, and translucent. Protoconch anastrophic, initially 2 prostrate, sinistral whorls, followed by an inflated smooth whorl normally placed on the summit. Mature whorls 16, short, slightly rounded and restricted at the sutures. Sculpture as in *C. porrecta*, both axial ribs and intercostal grooves stopping abruptly at the periphery, but the ribs narrower and more numerous, averaging about 20 to the whorl. Aperture also as in *C. porrecta*, the anterior margin sharply angled with the inner margin, which is straight and narrowly reflected. Length 12 mm.

Localities.—Bowen (J. Laseron), holotype and numerous paratypes; 1–3 fm Port Curtis (J. Laseron); Lady Elliott Island (C. Hedley).

Remarks.—The three species *C. gabrieli*, *C. porrecta*, and *C. queenslandica* are obviously closely related, but progressively are larger, have a wider apical angle, and more numerous axial ribs. Even when mixed from one locality there is no difficulty in their separation.

CHEMNITZIA OBLIQUA, sp. nov.

Figs. 164 and 165

Shell very small, nearly cylindrical, slender, elongated, white. Protoconch anastrophic, prostrate on summit, of 2 whorls. Mature whorls 8, rather long, slightly rounded and restricted at the sutures. Sculpture of thin, very oblique axial ribs, about their own distance apart, about 18 to the whorl, stopping abruptly on periphery, base smooth. Aperture extended anteriorly, outer and anterior margins rounded, the latter making a sharp angle with the inner margin, which is straight and narrowly reflected. Length 3·3 mm.

Localities.—4–14 fm Albany Passage (C. Hedley), holotype; Darwin (J. Laseron); 20 fm off Endeavour Reef (A. McCulloch).

Remarks.—This is a small, narrow species, resembling *C. gabrieli* in some characters, but the whorls are relatively longer, the axial ribs thinner and more oblique, and the intercostal grooves less deeply excavated. The Darwin specimens are rather larger than the type and relatively a little broader, but otherwise conform in essential characters. A specimen from Endeavour Reef is even more cylindrical than the type, the first whorl small, the remaining 6 practically equal.

Genus PYRGISCUS Philippi

Type species designated by Dall and Bartsch *Melania rufa* Philippi.
Pyrgiscus Philippi, 1841, p. 50.

Shell like *Turbonilla*, elongate, and with no fold on the inner margin of the aperture, and with axial ribs which are continuous to or fade on the base, but with the addition of spiral threads crossing the intercostal grooves.

PYRGISCUS CONFUSUS (Brazier)

Fig. 166

Turbonilla confusa Brazier, 1877, p. 258.
Turbonilla confusa Brazier. Hedley, 1901, p. 125.

Hedley in reviewing the types of the *Chevert* Expedition synonymized *Turbonilla rhabdoides* Watson under *confusa*, and accordingly did not figure the type of *confusa* as he did the remainder of Brazier's species. Examination of the type, which is in the Macleay Museum, Sydney University, shows it to be imperfect and rather worn, but still with sufficient character for specific determination. It is 7 mm long. One of two perfect specimens from 20 fm off Endeavour Reef (A. McCulloch), 5·8 mm in length, is here figured. Compared with the type it is slightly smaller and relatively narrower, but otherwise conforms in all characters. Compared with specimens identified from Watson's description and figure as *rhabdoides* it is a larger and more robust species with less rounded whorls, and with the axial ribs larger and closer together. *P. rhabdoides* is now restored to literature.

PYRGISCUS RHABDOIDES (Watson)

Figs. 167–169

Odostomia (*Turbonilla*) *rhabdoides* Watson, 1886, p. 492, pl. 32, fig. 5.

The type came from 28 fm west of Cape York, and its length is given as 0·19 in. (4·8 mm). Watson's excellent figure and full description make its identification relatively easy. The only doubt is whether Hedley (1901, p. 125) was correct in synonymizing it under *T. confusa* Brazier. For reasons already given it is thought *rhabdoides* should be retained, as it is evidently a smaller and more delicate species with more rounded ribs, which are thinner and more widely separated. Two specimens are here figured: Figure 168 from 4–14 fm Albany Passage (C. Hedley), very close to the type locality, and Figure 167 from 1–3 fm Port Curtis (J. Laseron) on the

Queensland coast well to the south. Figure 168 is 4 mm in length and Figure 167 5 mm. Other specimens are from Darwin (J. Laseron). Throughout this wide range, the species is reasonably constant, and the figures show about the extremes in variability.

Genus PYRGISCILLA Laws

Type species *Turbonilla chattonensis* Marwick.
Pyrgiscilla Laws, 1937*c*, p. 172.

Laws proposed and separated *Pyrgiscilla* from *Pyrgiscus* on the same grounds that *Chemnitzia* is separated from *Turbonilla*, that is the axial ribs stop abruptly at the periphery instead of being continuous on the base. In some species the axial threads crossing the intercostal spaces terminate in line with the axial ribs, leaving the base of the body whorl smooth, in others they continue uninterrupted to encircle the base.

PYRGISCILLA PROCERITA, sp. nov.

Fig. 170

Shell of medium size, elongate and acuminate, lower portion of spire almost cylindrical, the last 5 whorls nearly equal, white. Protoconch anastrophic, nearly planoid in coiling, tilted downwards on summit. Mature whorls 11, rounded, restricted at the sutures. Sculpture of rounded axial ribs, about their own width apart, 12–14 to the whorl, ceasing abruptly at the periphery, spiral sculpture of fine threads crossing the intercostal spaces, base of body whorl smooth. Aperture short, extended anteriorly, outer and anterior margins rounded, anterior margin making an angle with the inner margin, which is straight and narrowly reflected. Length 6·5 mm.

Localities.—Darwin (J. Laseron), holotype; Green Island off Cairns (C. Hedley); 5–10 fm Hope Islands (C. Hedley).

Remarks.—This can be easily distinguished from the other species here discussed by its narrow, elongate form, larger size, and more numerous whorls, as well as by details of the sculpture.

PYRGISCILLA INDENTA, sp. nov.

Fig. 171

Shell small, elongate, regularly conical, white. Protoconch anastrophic, small, prostrate on summit, of two whorls, the second inflated. Mature whorls 8, flattened and medially indented, not restricted at the sutures. Sculpture of strong, rounded axial ribs, rising above the sutures, about their own width apart, 16 to the whorl, terminating at the periphery. Spiral sculpture of fine threads crossing the intercostal spaces, and continuous on the base, which anteriorly is slightly hollowed. Aperture anteriorly extended, outer margin indented, anterior margin rounded, making an angle with the inner margin which is nearly straight and narrowly reflected. Length 3·5 mm.

Locality.—15 fm Palm Islands (C. Hedley), holotype and seven paratypes.

Remarks.—This is easily distinguished from other species of *Pyrgiscilla* by its flattened and indented whorls, but it can be confused with *Exesilla latacosta*, previously described, though it is slightly narrower, and the axial ribs are not quite so large. The main difference is of course the absence of a columella fold and the presence of spiral sculpture which is generic as well as specific, but the spiral sculpture disappears with the slightest wear, and unless the material is perfect, the two species are very hard to tell apart.

PYRGISCILLA CHEVERTI (Hedley)

Figs. 172 and 173

Turbonilla eximia Brazier, 1877, p. 257.
Turbonilla cheverti Hedley, nom. nov. for *eximia* Brazier (preocc.), 1901, p. 124, pl. 16, fig. 13.

The figure is taken from the holotype in the Macleay Museum, Sydney University, and is 4 mm in length. It came from the Percy Islands, Torres Straits. Several specimens from Port Curtis (J. Laseron) conform very closely to the type, and the species shows little variation over this considerable distance. A further locality is 20 fm off Endeavour Reef (A. McCulloch). It is a very distinctive little species, the cylindrical spire and well-rounded whorls giving it a definite facies.

PYRGISCILLA HOMOEATATA (Watson)

Figs. 174–176

Odostomia (*Turbonilla*) *homoeatata* Watson, 1886, p. 490, pl. 32, fig. 3.

The type locality is 7 fm Flinders Passage. It is a rather variable species, close to *P. cheverti* but conical and not cylindrical in form, with less rounded whorls, and fewer and broader axial ribs. It is common in the Torres Straits, and from a long series from 4–14 fm Albany Passage (C. Hedley), Figure 174 was selected as nearest to Watson's figure. It is also common from 20 fm Endeavour Reef (A. McCulloch). From this locality two specimens were picked out with rather a different form and larger than the typical specimens. One is here figured for comparison (Fig. 176). It is 4·6 mm in length.

PYRGISCILLA DIPSYCHA (Watson)

Fig. 177

Odostomia (*Turbonilla*) *dipsycha* Watson, 1886, p. 494, pl. 32, fig. 8.

The type locality is 28 fm west of Cape York. A number of specimens from 4–14 fm Albany Passage (C. Hedley) have been identified with some difficulty as this species, as it is apparently rather variable in form and width. In fact Watson separated the narrower individuals as var. *incerta*, var. nov., but this name is not perpetuated as the variation seems merely individual, and does not suggest a distinct race or subspecies. The specimen figured is 3 mm in length. Compared with *P. homoeatata* from the same locality, it is on the whole narrower and more cylindrical, the whorls are not so rounded, and the spiral sculpture is coarser and more distinct. In form it is more like *P. cheverti* but the axial ribs are fewer and larger, and again the whorls are less rounded.

PYRGISCILLA BIRESTIS, sp. nov.

Fig. 178

Shell minute, nearly cylindrical, white. Protoconch anastrophic, small, discoidal, tilted slightly downwards on the summit. Mature whorls 5, well rounded and restricted at the sutures. Sculpture of raised, rounded, oblique axial ribs, about their own width apart, 16 to the whorl, stopping abruptly at the periphery, spiral sculpture of two strong cords or narrow ribs on the earlier whorls, three on the body whorl, base smooth. Aperture extended anteriorly, outer and anterior margins rounded. the latter subangular with the inner margin, which is straight and narrowly reflected. Length 2 mm.

Locality.—20 fm off Endeavour Reef (A. McCulloch), holotype and two paratypes.

Remarks.—This is the smallest species of *Pyrgiscilla*, and its cylindrical shape, few whorls, and distinctive sculpture should facilitate its future recognition.

PYRGISCILLA LINEARIS, sp. nov.

Fig. 179

Shell of medium size, elongate, regularly conical, white. Protoconch in type missing. Remaining whorls 10, nearly flat, not restricted at the sutures. Sculpture of broad, rounded, straight axial ribs, less than their own width apart, 14 to the whorl, stopping abruptly just below the periphery. Spiral sculpture consisting of narrow grooves crossing the intercostal spaces, 6 or 7 to the whorl, base of body whorl smooth. Aperture extended anteriorly, outer margin nearly straight, anterior margin rounded, inner margin nearly straight and evenly reflected. Length 6 mm.

Locality.—Darwin (J. Laseron), holotype.

Remarks.—This species is founded on a single specimen without the protoconch, but its characters are so distinctive that there should be no difficulty in its future recognition. The spiral sculpture of distant grooves instead of raised threads separates it from all the species here discussed. It is nearest in other characters to *P. procerita*, but has much flatter whorls and the axial ribs are broader and straighter, and the body whorl is relatively longer. In form it resembles *Exesilla aplini* (Brazier), but the presence of spiral sculpture and the absence of a columella fold are generic as well as specific differences.

Genus MORMULASTA, gen. nov.

Type species *Mormulasta iredalei*, sp. nov.

Mormulasta is proposed for elongated, many-whorled shells, like *Pyrgiscilla* in having both axial and spiral sculpture, but with the spiral sculpture in the form of incised lines which override the axial ribs and break them into elongated lozenges (see Fig. 181). Another characteristic is the presence of varices, irregularly disposed on the spire.

Dall and Bartsch (1904, 1909) made these varices a major characteristic, and used *Mormula* A. Adams for a number of West American shells which may be related or even congeneric with *Mormulasta*. Reference to *Mormula* A. Adams (1864, p. 1), the type species of which came from Japan, shows a singular and very different shell, banded, very like *Rissoina*, but with a sinistral protoconch, and with the inner lip of the aperture spirally twisted. Certainly neither the west American shells placed in *Mormula* nor the Australian *Mormulasta* can be considered congeneric with the Japanese type.

MORMULASTA IREDALEI, sp. nov.

Figs. 180–182

Shell large, elongate, conical, colour yellow-brown, spirally banded in various shades of brown, a darker band below the sutures. Protoconch anastrophic, planoidly coiled, tilted on summit. Mature whorls 12, slightly rounded and restricted at the sutures. Sculpture of broad, rounded axial ribs, close together, separated by narrow deep grooves, about 20 to the whorl, one rib on the body whorl enlarged to a broad varix, the ribs fading on the base. Spiral sculpture of incised grooves which cross the axial ribs only, breaking them into oval lozenges. Below the termination of the axial ribs on the body whorl, the spiral sculpture continues as incised grooves on the base. Aperture extended anteriorly, outer margin rounded and indented by the spiral sculpture, anterior and inner margins rounded, the latter narrowly reflected. Length 15 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype and number of paratypes; Murray Island, common.

Remarks.—This is one of the few coloured species of the Turbonillinae, and its large size and distinctive sculpture also make it easily recognizable.

MORMULASTA sp.

Fig. 183

A single specimen of what is almost certainly another species of *Mormulasta* was collected by J. Laseron at Bowen, but more material is needed to verify its specific determination. Compared with *M. iredalei* it is much smaller, only 4·7 mm in length, the lower portion of the spire is more cylindrical, the whorls are slightly more rounded, and the anastrophic protoconch is not planoidly coiled. The sculpture is, however, practically identical. It is here figured for future reference.

Genus ZAPHELLA, gen. nov.

Type species *Turbonilla tribulationis* Hedley.

Zaphella is proposed for a group of species which, like *Chemnitzia*, have no spiral sculpture, and in which the axial ribs stop short at the periphery. But the species are relatively shorter and with fewer whorls, and the axial ribs rise above the summits of the whorls, where they become swollen and tubercular, and may be joined by a spiral rib. In nearly all the species also the summits of the whorls are stepped.

ZAPHELLA NODULOSA, sp. nov.

Fig. 184

Shell of medium size, solid, elongate, relatively broad, spire slightly convex, opaque, colour a creamy white. Protoconch unknown. Mature whorls 8, very slightly rounded, not restricted at the sutures, base curved into a narrow umbilical slit. Sculpture of strong, rounded, closely packed, oblique axial ribs, about 26 to the whorl, separated by narrow, deeply excavated channels, terminating abruptly just below the periphery, connected just below the suture by a spiral keel, above which the axial ribs rise in rounded tubercles extending above the sutures, the base of the body whorl smooth. Aperture extended anteriorly, the outer margin indented, anterior margin rounded, inner margin curved and narrowly reflected. Length 7·5 mm.

Locality.—4–14 fm Albany Passage (C. Hedley), holotype.

Remarks.—Though founded on a single specimen, this is such a striking species that its distinctive form, closely packed axial ribs, and the row of tubercles below the sutures should make its future recognition easy.

ZAPHELLA TROPICA, sp. nov.

Fig. 185

Shell minute, conical with an even spire, white. Protoconch anastrophic, prostrate on summit, of two whorls, the first small, the second inflated. Mature whorls 6, relatively long, slightly rounded, restricted below the sutures. Sculpture of well-defined, rounded axial ribs, slightly oblique, about their own width apart, 16 to the whorl, ending abruptly at the periphery, rising in nodules above a broad, subsutural spiral rib, the base of the body whorl smooth and rounded. Aperture slightly extended anteriorly, outer and anterior margins rounded, inner margin short and rounded, very narrowly reflected. Length 2·6 mm.

Localities.—20 fm off Endeavour Reef (A. McCulloch), holotype; 15 fm Palm Islands (C. Hedley); Darwin (J. Laseron); 4–14 fm Albany Passage (C. Hedley); Port Moresby (J. Laseron).

Remarks.—The row of subsutural beads make this species easy to distinguish from other small species with which it may be confused. Compared with *Z. nodulosa*, it is much smaller, has a different form, and the axial ribs are fewer, less oblique, and farther apart.

ZAPHELLA SUBCARINA, sp. nov.

Fig. 186

Shell small, regularly conical, white. Protoconch anastrophic, prostrate on summit, of two whorls, the first small, the second inflated. Mature whorls 8, slightly rounded, not restricted at the sutures. Sculpture of well-defined, flexuous, rounded axial ribs, more than their own width apart, 14 to the whorls, terminating abruptly at the periphery, and rising at the summit of the whorls above a distinct subsutural spiral keel, the intercostal grooves deeply excavated. Aperture extended anteriorly, outer margin flexuous, anterior margin rounded, inner margin curved and narrowly reflected. Length 3 mm.

Locality.—1–3 fm Port Curtis (J. Laseron), holotype and four paratypes.

Remarks.—Comparison with *Z. tropica*, which the species generally resembles, shows that the axial ribs are fewer and farther apart, they are flexuous, and where they rise above a subsutural keel they are not nodulose.

ZAPHELLA TRIBULATIONIS (Hedley)

Figs. 187–189

Turbonilla tribulationis Hedley, 1909, p. 450, pl. 42, figs. 79–80.

The type locality is the Hope Islands. The specimen here figured (Fig. 187) is from 4–14 fm Albany Passage (C. Hedley), and is 4·4 mm in length, rather larger than the type, but otherwise conforming to the specific description. It has been selected as the type of the genus because it shows the extreme divergence from the nearest genus *Chemnitzia*. Its stepped whorls and rhomboidal aperture give it a distinctive facies.

A single specimen (Fig. 189) from Port Curtis (T. Iredale) differs in detail from the type, but may not be quite mature, and more material is needed to decide if it is a distinct species or merely an individual variation. It is 3·2 mm in length. It is here figured for future reference.

ZAPHELLA VINCULA, sp. nov.

Figs. 190 and 191

Shell small, broadly conical, spire slightly convex, white. Protoconch anastrophic, the sinistral portion nearly planoid, at right angles to the main axis, followed by a short, smooth dextral whorl. Mature whorls 5, flattened, narrowly shelved at the summits, body whorl slightly excavate at the base. Sculpture of numerous, raised, rounded axial ribs, less than their own width apart, about 24 to the whorl, stopping abruptly at a narrow spiral keel on the periphery, but not nodulose at the summits of the whorls, base of body whorl smooth. Aperture well produced and narrowed and reflected anteriorly, outer and anterior margins rounded, inner margin long, slightly curved and reflected. Length 3·2 mm.

Locality.—4–14 fm Albany Passage (C. Hedley), holotype.

Remarks.—The type may not be quite mature, but its characters are so distinctive that there should be no difficulty in its future recognition. Superficially it resembles *Z. tribulationis*, but has a different protoconch, is broader in relation to its length, the whorls are more narrowly shelved, the axial ribs are not nodulose at their summits, and terminate on the periphery at a narrow spiral rib. These characters suggest that ultimately it may be found to have quite different relationship.

Genus AMAMIMORMULA Kuroda

Type species *Turbonilla belonis* Melvill & Standen.
Amamimormula Kuroda, 1928, p. 80.

This genus, based on *Turbonilla belonis* Melvill & Standen (1896, p. 303, pl. 10, fig. 56) from Lifu, is applied to a distinctive Queensland shell which has the form and mainly the sculpture of *Chemnitzia*, but below the abrupt termination of the axial ribs on the periphery there is a strong spiral keel, which is visible also on the earlier whorls, just above the suture. The Queensland species is closely related to *A. belonis*, but differs sufficiently to warrant description as a new species.

AMAMIMORMULA TORRESIANA, sp. nov.

Figs. 192 and 193

Shell relatively large, slender, conical, and elongate, colour of type pale yellow, other specimens white. Protoconch anastrophic, nearly spherical, at right angles to the summit. Mature whorls 13, short, rounded, restricted at the sutures. Sculpture of narrow, raised, rounded axial ribs, more than their own width apart, about 24 to the whorl, terminating on the early whorls above and short of the sutures, and on the body whorl at the periphery, below them a strong, rounded spiral rib, the base of the body whorl slightly excavate. Aperture short, not extended anteriorly, the outer and anterior margins rounded, inner margin curved and narrowly reflected. Length 11 mm.

Localities.—Murray Island, holotype; Rocky Isle, Cape Flattery (C. Hedley).

Remarks.—The distinctive sculpture at once separates this both specifically and generically from all other known Australian members of the family. It is evidently closely related to *Amamimormula belonis* (Melvill & Standen) from Lifu, but it is larger, relatively narrower, has more numerous axial ribs, and no denticles within the outer margin of the aperture.

Genus CINGULINA A. Adams

Type species by monotypy *Cingulina circinata* A. Adams.
Cingulina A. Adams, 1860*c*, p. 414.

Cingulina seems a natural genus, the main characteristics of which are a long, conical, acuminate shell with many short whorls, sculpture of strong spiral ribs, with axial striations in the interstices, and with a simple aperture without a columella fold. The type species came from Japan.

Two species only have so far been identified from Queensland, but fragments have been seen from various localities which may prove to be additional species.

CINGULINA AUSTRINA, sp. nov.

Figs. 194–196

Shell of medium size, conical, elongate and acuminate, thin, white, shining, and slightly translucent. Protoconch small, anastrophic, almost spherical, half immersed in about half the summit. Mature whorls in type 8, but varying to 9 or 10, flattened, sutures narrowly channelled and discernible. Sculpture of broad, flattened spiral ribs, 3 to the whorl, the uppermost slightly rounded, narrower than the other two, which are flatter and separated by a very narrow channel which is generally little more than an incised line. Aperture short, slightly extended anteriorly, the outer margin indented by the sculpture, the anterior margin rounded, angled with the inner margin, which is straight, and narrowly reflected. Length of holotype 5·6 mm, other specimens up to 8 mm, others smaller.

Localities.—Peel Island, Moreton Bay (Mrs. J. Kerslake), holotype (Fig. 194) and numerous paratypes; Caloundra (Fig. 195); 1–3 fm Port Curtis (J. Laseron) (Fig. 196); and numerous localities in the Peronian province.

Remarks.—This is the species which has previously been known from New South Wales as *C. circinata* A. Adams, the type of which came from Japan. The true *circinata*, however, has narrower, more elevated, rounded spiral ribs, separated by deep channels, and is actually closer to the common Peronian species *C. spina* Crosse & Fischer than to the species now described. *C. australis* is slightly variable, both in size and relative width, and in some species the furrows between the ribs are deeper than in others. Figure 196 is a juvenile which has rather a different facies from the adult shell.

CINGULINA IMPERITA, sp. nov.

Figs. 197 and 198

Shell relatively large, narrowly conical, elongate and acuminate, white, surface shining. Protoconch anastrophic, a small, almost spherical sinistral stage, followed by a normal, smooth dextral whorl. Mature whorls 14, short, increasing regularly, the sutures channelled but barely distinguishable from the grooves separating the spiral ribs, base of body whorl flattened. Sculpture of well-raised, prominent spiral ribs, 3 to the whorl, about their own width apart, the lower two equal, the uppermost the smallest. Aperture short, well extended anteriorly, the outer margin indented by the sculpture, anterior margin sharply angled with the inner margin, which is thickened, nearly straight but slightly sinuous. Length 13·8 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype; Peel Island, Moreton Bay (Mrs. J. Kerslake).

Remarks.—This is apparently a fairly common species in southern Queensland, though perfect specimens have been hard to obtain. The inequality of the spiral ribs is, however, a distinctive character, and even fragments are easy to recognize.

Genus KOLOONELLA, gen. nov.

Type species *Eulimella moniliformis* Hedley.

Elongated, thin, fragile shells, vitreous and translucent in texture, with more or less rounded whorls, without sculpture, apertures simple without any columella fold. The anastrophic protoconch is generally very exsert, the stage between sinistral and dextral coiling often prolonged as a short, nearly straight tube.

The systematic position of a number of Australian species hitherto included in *Eulimella* Forbes has always been in doubt. They come broadly within the general description of *Eulimella*, but this European genus has quite a different texture, being solid and porcellanous, with short whorls, more in appearance like *Syrnola*, though without a columella fold. There is probably very little, if any, actual relationship between *Koloonella* and *Eulimella*. All the southern species previously included in *Eulimella* should now be transferred to *Koloonella*.

KOLOONELLA CAPRICORNIA, sp. nov.

Fig. 199

Shell small, conical, elongate, acuminate, thin and fragile, colourless, glassy, and translucent. Protoconch exsert, elongate, anastrophic, oblique on the summit, sinistral portion small and discoidal. Mature whorls 6, long, flattened, with slightly rounded shoulders. Sculpture absent, except for faint, microscopic growth lines. Aperture slightly extended, outer margin nearly flat with a rounded shoulder, anterior margin round, inner margin curved, very narrowly reflected. Length 3·2 mm.

Localities.—Bowen (J. Laseron), holotype and two paratypes; Peel Island, Moreton Bay (Mrs. J. Kerslake); Darwin (J. Laseron).

Remarks.—This species resembles *K. moniliformis* (Hedley), in form, size and protoconch, but has uniformly flatter whorls, and the slightly rounded whorls give it a distinct facies. It can be considered the northern equivalent of the Peronian *moniliforme*, and no doubt will be found in the intermediate localities throughout its extensive range.

KOLOONELLA LAXA (Watson)

Fig. 200

Eulimella laxa Watson, 1886, p. 497, pl. 33, fig. 6.

The type locality is 155 fm off Raine Island, the length of the type given 0·085 in. (2·2 mm). It is reidentified with a little uncertainty, but a specimen from 4–14 fm Albany Passage (C. Hedley) is close to Watson's figure and description, though it has an extra whorl, and is not quite so cylindrical in form. The long body whorl seems a good guide to its recognition. The length of the specimen figured is 2·5 mm.

KOLOONELLA sp.

Fig. 201

A minute species from Bowen (J. Laseron) is almost certainly an undescribed species, but more and better material is required before its identity can be established. It is here figured for future reference. Its length is only 1·5 mm, and if mature it is the smallest of the species here discussed. The texture, as in the other species, is thin, glassy, and transparent.

KOLOONELLA SUBTILIS (Watson)

Figs. 202 and 203

Eulimella subtilis Watson, 1886, p. 499, pl. 33, fig. 5.

The type locality is 3–11 fm Torres Straits, the length of the type 0·12 in. or approximately 3 mm. The species is again identified with a little uncertainty, as specimens examined are a little more cylindrical in form than shown in Watson's figure. Figure 202 is from 4–14 fm Albany Passage (C. Hedley), and is 2·1 mm in length, rather smaller than the type, and with two whorls less. Specimens from Darwin (J. Laseron) have 6 whorls, one less than the type, are larger, but are very close to it in form. That figured (Fig. 203) is 3·5 mm in length. The long body whorl and flat whorls are taken as characteristic of this species.

KOLOONELLA TENUIS, sp. nov.

Fig. 204

Shell very small, nearly cylindrical, narrow and elongate, very thin and fragile, colourless, vitreous, and transparent. Protoconch small, anastrophic, apparently planoid. Mature whorls 7, slightly rounded and restricted at the sutures. Sculpture none, the surface smooth and shining, the texture quite transparent so that the columella is visible from the exterior. Aperture small and extended anteriorly, all the margins rounded, the inner margin very narrowly reflected. Length 2·8 mm.

Locality.—Port Moresby (J. Laseron), holotype and three paratypes.

Remarks.—This species is nearest to *K. subtilis*, but is narrower and even more cylindrical, and the whorls are more rounded.

Genus PARADOXELLA, gen. nov.

Type species *Paradoxella ambigua*, sp. nov.

This genus is proposed for an elongated, white, smooth shell with a true anastrophic protoconch which takes it into the Pyramidellidae, but a semicircular and laterally extended aperture which recalls the Rissoinidae. The outer margin of the aperture when laterally viewed is also posteriorly sinuate. Were it not for the protoconch this unique species might well be considered as an undescribed *Morchiella*, a genus of the Rissoinidae.

PARADOXELLA AMBIGUA, sp. nov.

Figs. 205–207

Shell of medium size, elongate and acuminate, the lower portion of the spire cylindrical, the last 4 whorls practically equal. Protoconch anastrophic, at right angles to the summit, flattened, and planoidly coiled. Mature whorls 11, slightly rounded and restricted at the sutures. Sculpture absent, the surface smooth except for a slight, spiral swelling below the sutures, and a few obscure, irregularly developed axial threads. Aperture semicircular, not extended anteriorly, laterally expanded, the outer and anterior margins from in front rounded, the outer margin when laterally viewed curved forward with a shallow posterior sinus, the inner margin short, curved, thickened, and reflected. Length 9 mm.

Locality.—Low Isles (T. Iredale), holotype.

Remarks.—There is no other species of Pyramidellidae with which this can be compared, the sinuate outer margin of the aperture alone being a distinctive character. The facies is that of *Morchiella*, a genus of the Rissoinidae, but the protoconch distinguishes it from any member of that group.

Genus ZONELLA, gen. nov.

Type species *Odostomia* (*Turbonilla*) *amoebaea* Watson.

Shell elongate, with an anastrophic protoconch, a simple aperture without a columella fold, the surface smooth but with the whorls medially carinate and with a spiral rib at the sutures.

This is another of the Australian shells with distinctive characters which will not fit into any broad generic grouping. Even Watson, who was ultraconservative in his generic allocations, remarked when describing the type species: "I have very little doubt that this should belong to a separate genus, but until more is known of the group it is better to leave it in *Odostomia*."

ZONELLA AMOEBAEA (Watson)

Figs. 208 and 209

Odostomia (*Turbonilla*) *amoebaea* Watson, 1886, p. 495, pl. 33, fig. 1.

The type came from 3–11 fm Torres Straits, and the specimen here figured is from a near locality 4–14 fm Albany Passage (C. Hedley) where it is not uncommon. It is 3·2 mm in length. Other specimens studied came from 5–10 fm Hope Islands (C. Hedley); 15 fm Palm Islands (C. Hedley); Cape Sidmouth (A. U. Henn), and and Port Curtis (J. Laseron). Throughout this range it is remarkably constant, and Watson's excellent figure and description leave no doubt as to its identity.

ZONELLA COACTA (Watson)

Fig. 210

Eulimella coacta Watson, 1886, p. 498, pl. 33, fig. 4.

The type locality is 8 fm off Wednesday Island, the length of the type 0·148 in. (3·7 mm). The specimen figured is from 15–20 fm off Pt. Charles, Darwin (M. Ward), and is 3 mm in length. Specimens have also been examined from 4–14 fm Albany Passage (C. Hedley). In form this is very close to *Z. amoebaea*, but the texture is thinner, glassy, and translucent, the medial carination of the whorls is less marked, and the strong spiral rib at the suture is replaced by a less distinct swelling.

Genus INSTARELLA, gen. nov.

Type species *Instarella subcarina*, sp. nov.

Elongated shells like *Zonella*, with the whorls medially carinate, but without the spiral keel at the periphery. The carination is slight, but gives them a distinct facies, and separates them from *Koloonella*.

INSTARELLA SUBCARINA, sp. nov.

Figs. 211 and 212

Shell of medium size, elongate and attenuate, yellowish white, opaque. Protoconch anastrophic, relatively large, prostrate on the summit, of two whorls, the second inflated. Mature whorls 12, smooth and without sculpture, but angled about two-thirds from their summits, with flat sides sloping in to the sutures. A few faint axial plications are present on the body whorl. Aperture well extended anteriorly, the outer and anterior margins rounded, the latter making a sharp angle with the inner margin, which is straight and evenly reflected. Length 7·8 mm.

Localities.—1–3 fm Port Curtis (J. Laseron), holotype and one paratype; 4–14 fm Albany Passage (C. Hedley); 5–10 fm Hope Islands (C. Hedley).

Remarks.—There is no other Australian species with which this can readily be compared. From species of *Koloonella* which alone it broadly resembles it can readily be separated by its attenuate form and the angulation of the whorls.

INSTARELLA SUBANGULATA, sp. nov.

Fig. 213

Shell small, elongate, conical, acuminate, very thin and fragile, colourless, and translucent. Protoconch small, anastrophic, prostrate on summit. Mature whorls 8, restricted at the sutures, slightly rounded, subangular at about one-third below the sutures, the angulation more apparent on the early whorls. Sculpture not visible under low magnification, but at magnification above 40 × a narrow keel is visible at the angulation, and numerous, very fine, oblique axial threads, again more distinct on the earlier whorls. Aperture extended anteriorly, outer and anterior margins rounded, inner margin curved and very narrowly reflected. Length 3 mm.

Locality.—Darwin (J. Laseron), holotype and two paratypes.

Remarks.—In form and general appearance this is very similar to *Koloonella moniliformis* (Hedley), a common Peronian species, but it has a different protoconch, and the slight angulation of the whorls and the microscopic sculpture take it into a different genus.

V. NEW GENERA

New genera proposed in this paper are *Aphalista*, *Eurathea*, *Exesilla*, *Instarella*, *Koloonella*, *Kunopia*, *Mormulasta*, *Paradoxella*, *Parodostomia*, *Quirella*, *Tathrella*, *Urambella*, *Wingenella*, *Zaphella*, and *Zonella*.

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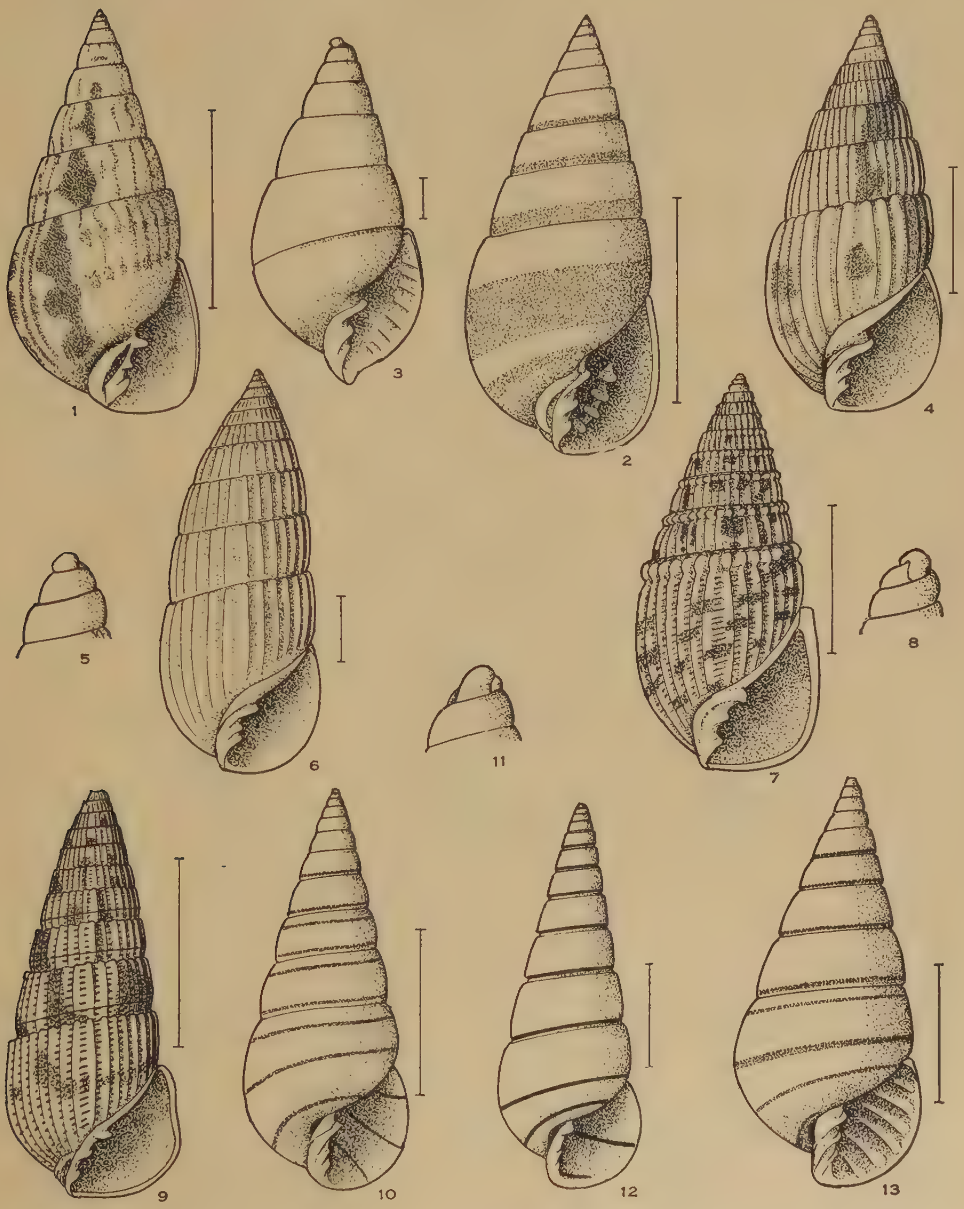

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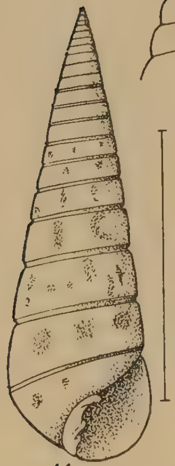
Fig. 1.—*Milda ventricosa* (Guerin). Fig. 2.—*M. cincta* (Reeve). Fig. 3.—*M. cincta* (?), juvenile. Fig. 4.—*Aphalista mitralis* (A. Adams). Fig. 5.—*A. mitralis*, protoconch. Fig. 6.—*A. mitralis*, variety. Fig. 7.—*Otopleura auriscati* (Dillwyn). Fig. 8.—*O. auriscati*, protoconch. Fig. 9.—*O. australis*, sp. nov., holotype. Fig. 10.—*Urambella ballerina*, sp. nov., holotype. Fig. 11.—*U. ballerina*, protoconch. Fig. 12.—*U. affinis*, sp. nov., holotype. Fig. 13.—*U. plicata*, sp. nov., holotype. The scale lines indicate the natural size of the specimens.



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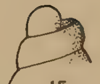

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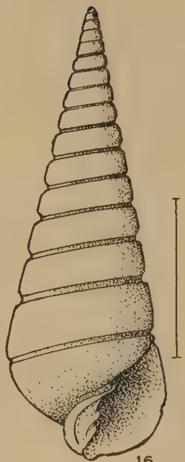

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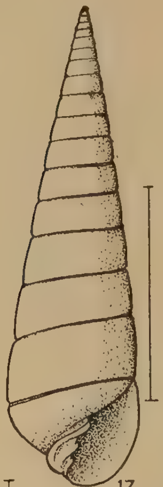

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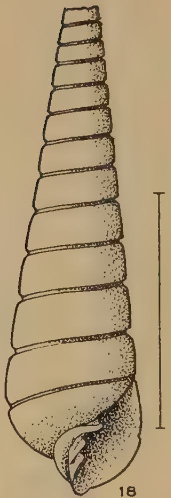

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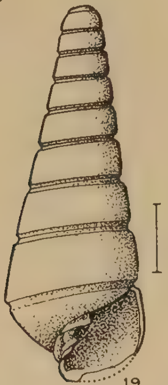

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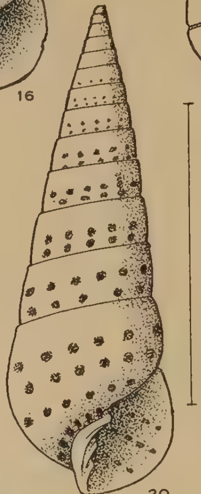

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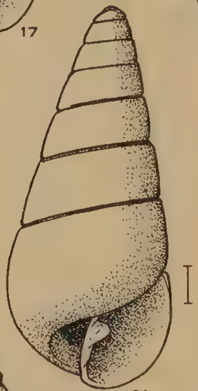

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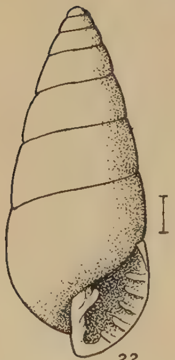

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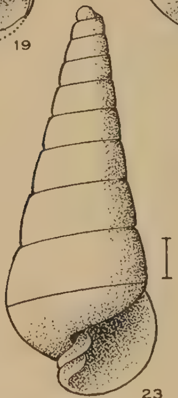

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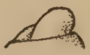

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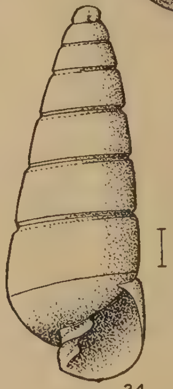

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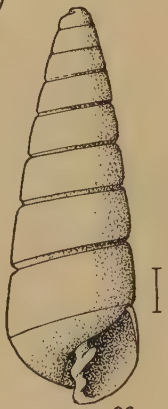

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Fig. 14.—*Wingenella eburnea*, sp. nov., holotype. Fig. 15.—*W. eburnea*, protoconch. Fig. 16.—*W. eburnea* (?), half grown. Fig. 17.—*W. pricena*, sp. nov., holotype., Fig. 18.—*W. pricena*, variation. Fig. 19.—*W. obtusa*, sp. nov., holotype. Fig. 20.—*Voluspa maculosa* (Lamarck). Fig. 21.—*Tiberia queenslandica*, sp. nov., holotype. Fig. 22.—*Cossmannica jacksonensis* (Dall & Bartsch). Fig. 23.—*C. exesa*, sp. nov., holotype. Fig. 24.—*C. subcarina*, sp. nov., holotype. Fig. 25.—*C. subcarina*, protoconch. Fig. 26.—*C. subcarina*, variation.

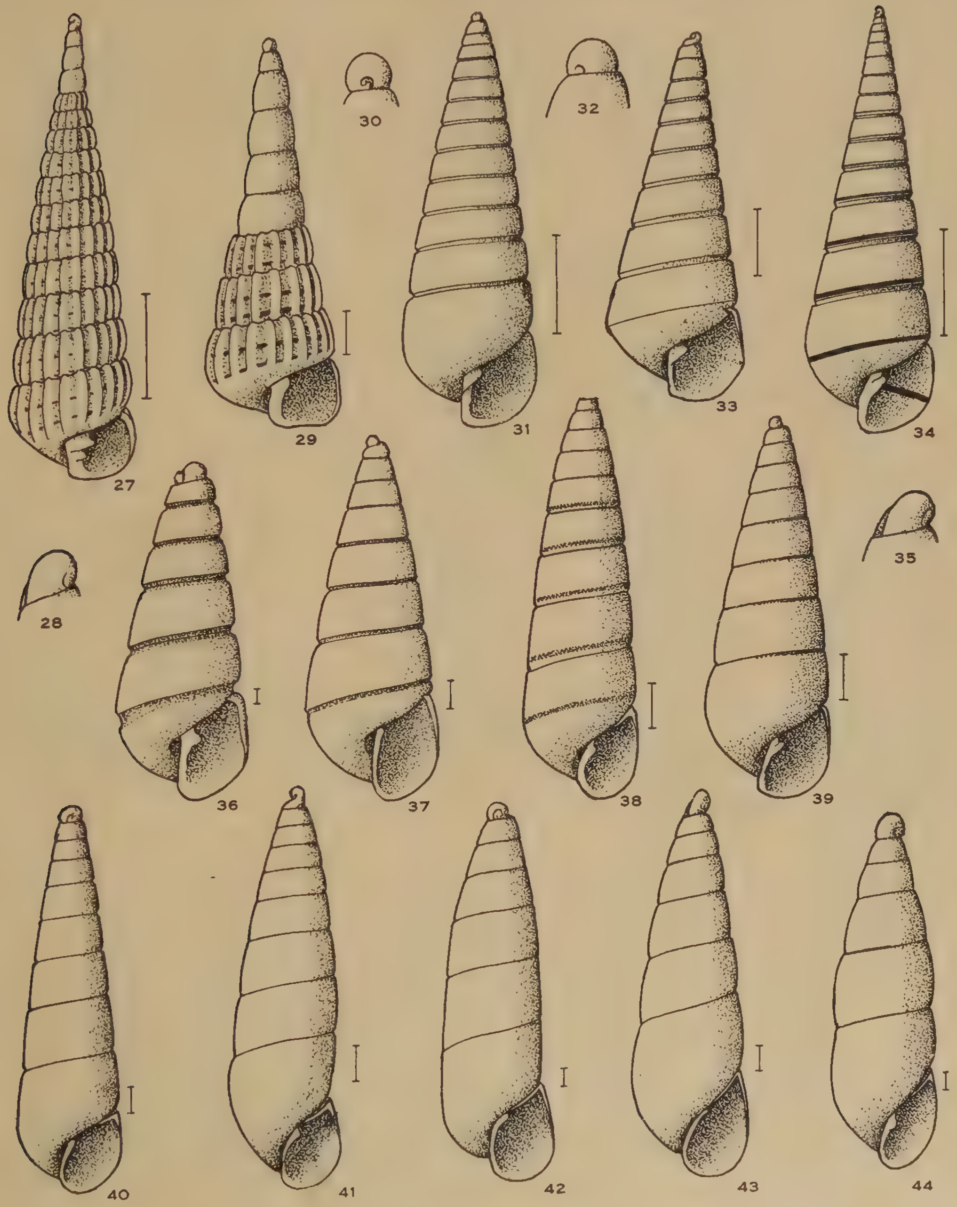

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Fig. 27.—*Tropaeas imperforata*, sp. nov., holotype. Fig. 28.—*T. imperforata*, protoconch. Fig. 29.—*T. imperforata*, juvenile. Fig. 30.—*T. imperforata*, protoconch. Fig. 31.—*Colsyrnola sericea* Iredale. Fig. 32.—*C. sericea*, protoconch. Fig. 33.—*C. translucida*, sp. nov., holotype. Fig. 34.—*C. margarita*, sp. nov., holotype. Fig. 35.—*C. margarita*, protoconch. Fig. 36.—*C. canaria* (Hedley), after Hedley. Fig. 37.—*C. canaria* (Hedley). Fig. 38.—*Syrnola pulchra* Brazier. Fig. 39.—*S. solanderiana*, sp. nov., holotype. Fig. 40.—*S. acerrima* (Watson). Fig. 41.—*S. torresiana*, sp. nov., holotype. Fig. 42.—*S. eruca*, sp. nov., holotype. Fig. 43.—*S. convoluta* (Watson). Fig. 44.—*S. convoluta*, juvenile.

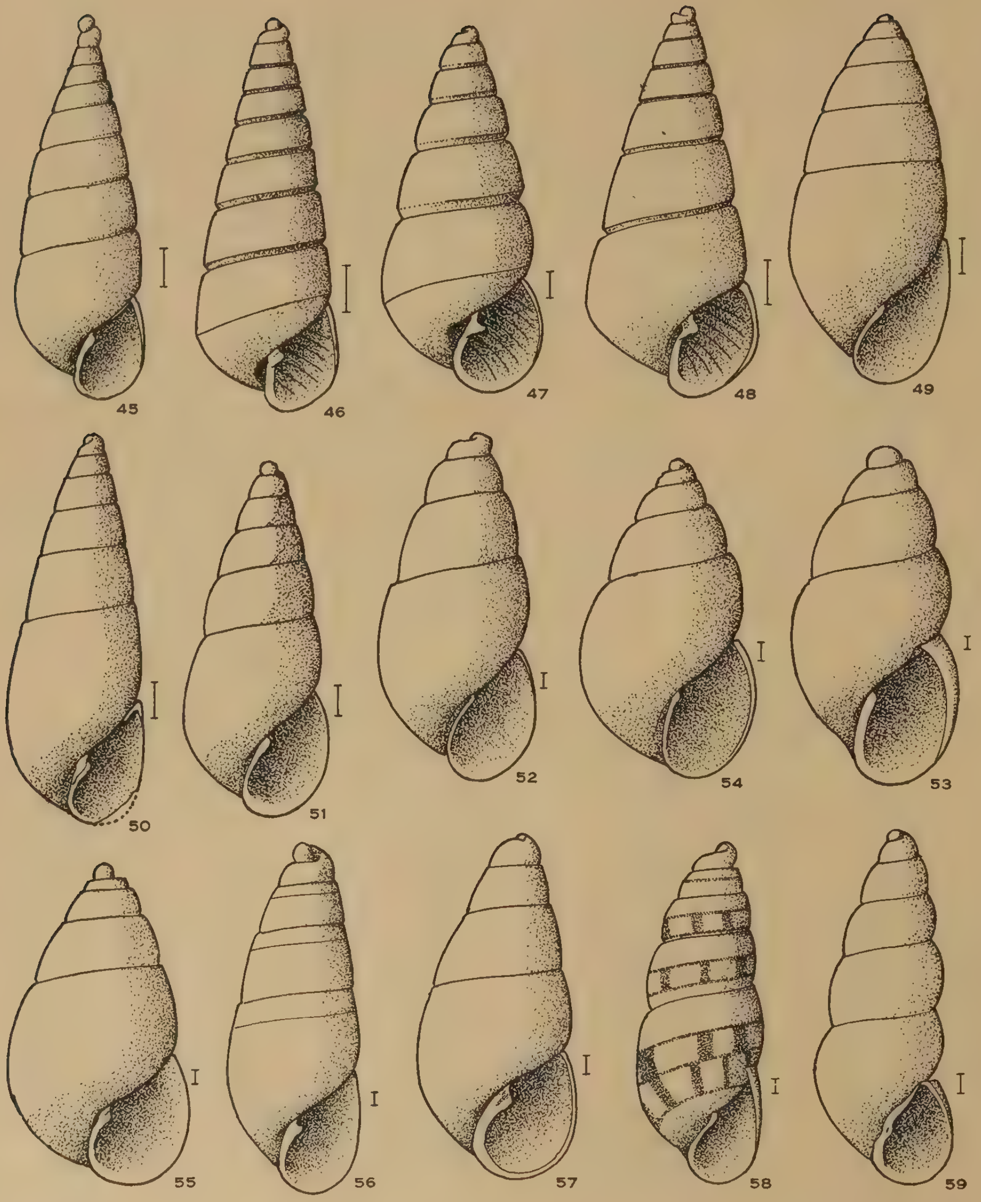

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Fig. 45.—*Syrnola exserta*, sp. nov., holotype. Fig. 46.—*Parodostomia compta* (Brazier). Figs. 47 and 48.—*P. compta*, variations. Fig. 49.—*Odostomia corpulenta* Watson, after Watson. Fig. 50.—*O. recta*, sp. nov., holotype. Fig. 51.—*O. clara* Brazier. Fig. 52.—*O. oxia* Watson. Fig. 53.—*O. oxia*, variation. Fig. 54.—*O. adiposa*, sp. nov., holotype. Fig. 55.—*O. adiposa*, variation. Fig. 56.—*O. mera*, sp. nov. holotype., Fig. 57.—*Odostomia* sp. Fig. 58.—*O. metata* Hedley, after Hedley. Fig. 59.—*O. sperabilis* Hedley, after Hedley.

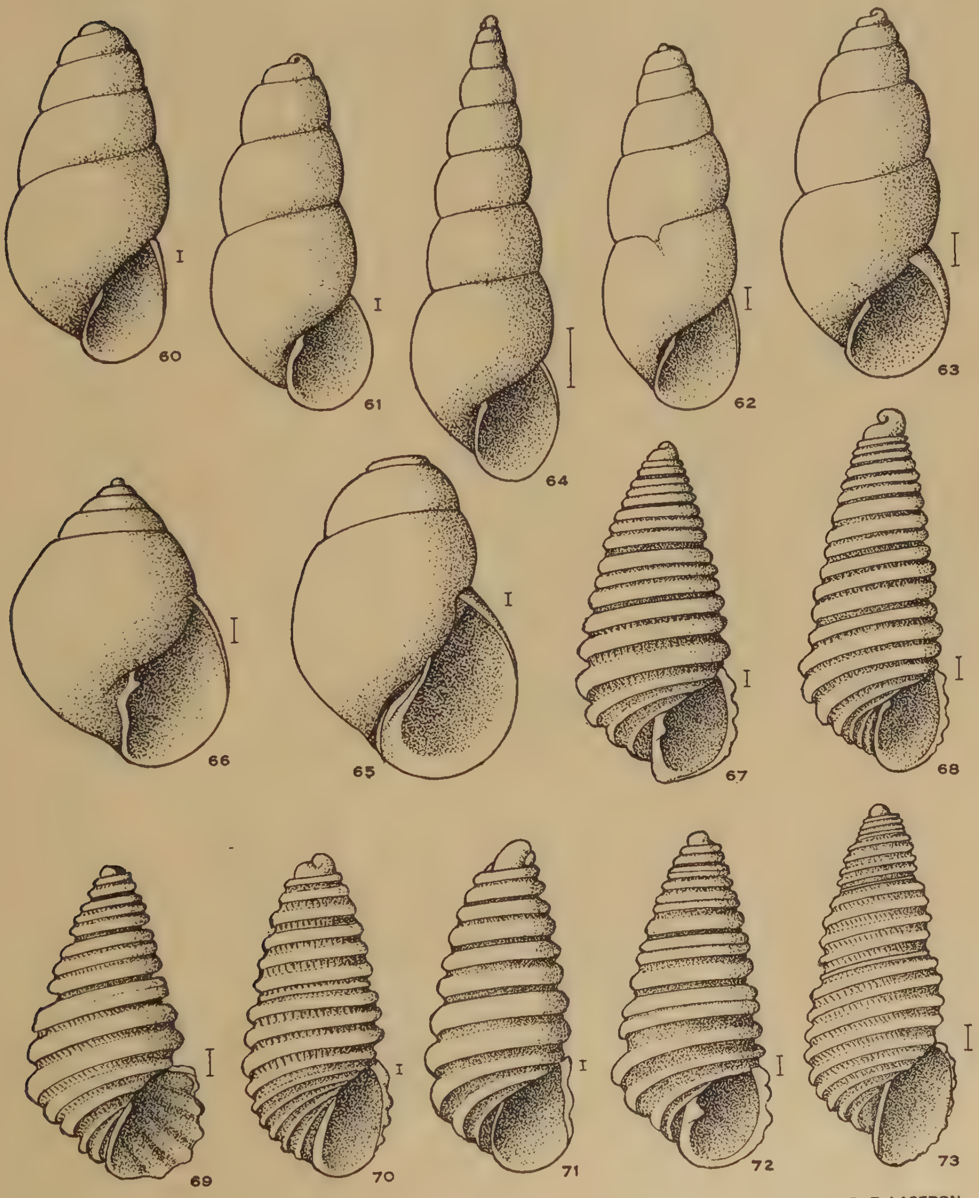

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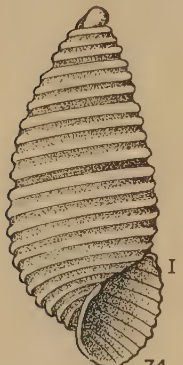
Fig. 60.—*Odostomia abjecta* Hedley, after Hedley. Figs. 61 and 62.—*O. abjecta*, variations. Fig. 63.—*O. stricta*, sp. nov., holotype. Fig. 64.—*O. eruca*, sp. nov., holotype. Fig. 65.—*O. anxia* Hedley, after Hedley. Fig. 66.—*O. bulbula* Hedley, after Hedley. Fig. 67.—*Hinemoa gumia* (Hedley). Fig. 68.—*H. migma* (Hedley). Fig. 69.—*H. sternerea*, sp. nov., holotype. Fig. 70.—*H. laquearia* (Hedley), after Hedley. Fig. 71.—*H. rubra*, sp. nov., holotype. Fig. 72.—*H. duplex*, sp. nov., holotype. Fig. 73.—*H. leviplex*, sp. nov., holotype.



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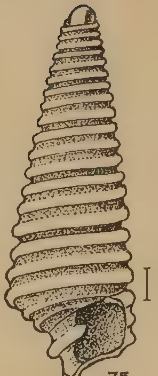

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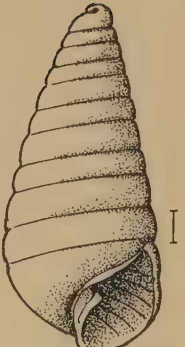

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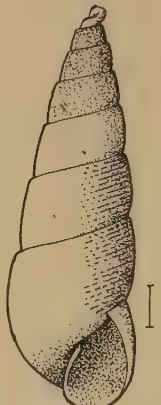

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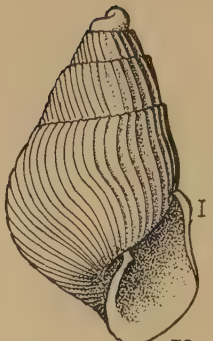

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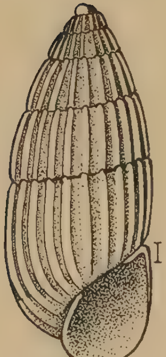

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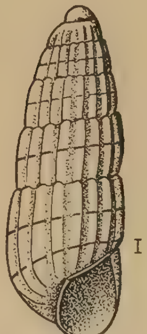

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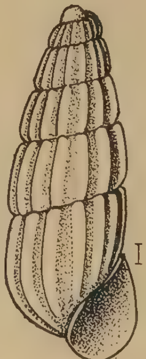

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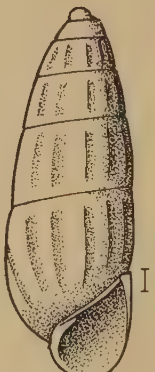

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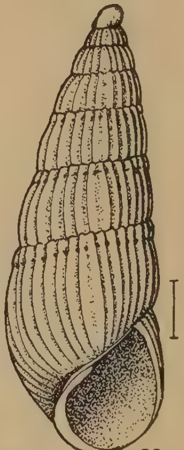

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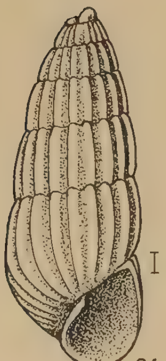

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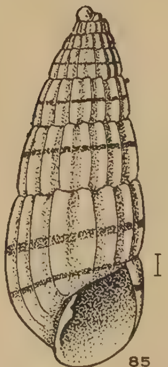

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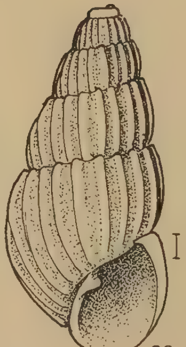

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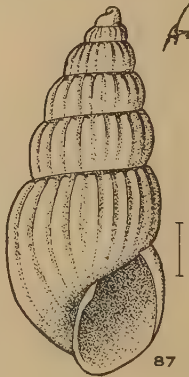

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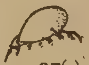

87(a)

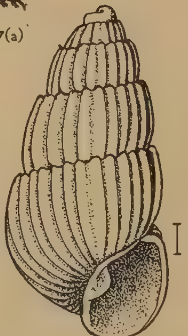

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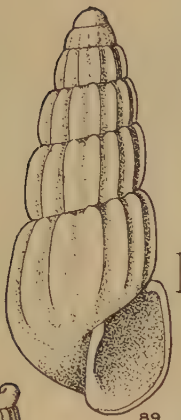
Fig. 74.—*Hinemoa voorwindei*, sp. nov., holotype. Fig. 75.—*Hinemoa* sp. Fig. 76.—*H. fossalina*, sp. nov., holotype. Fig. 77.—*Evalea queenslandica*, sp. nov., holotype. Fig. 78.—*Kunopia sigma* (Hedley), after Hedley. Fig. 79.—*Herviera gliriella* (Melvill & Standen). Fig. 80.—*H. chorea* (Hedley). Fig. 81.—*Herviera* sp. Fig. 82.—*H. pupa* (Watson), after Watson. Fig. 83.—*H. magis*, sp. nov., holotype. Fig. 84.—*Elodiamea kymatodes* (Watson). Fig. 85.—*E. fasciata*, sp. nov., holotype. Fig. 86.—*E. ora*, sp. nov., holotype. Fig. 87.—*E. caduca*, sp. nov., holotype. Fig. 87(*a*).—*E. caduca*, protoconch. Fig. 88.—*E. multicostata*, sp. nov., holotype.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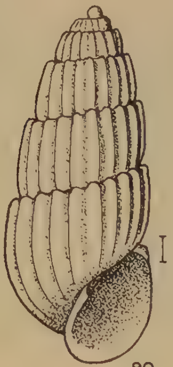
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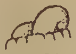
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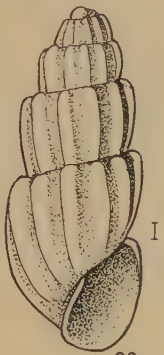
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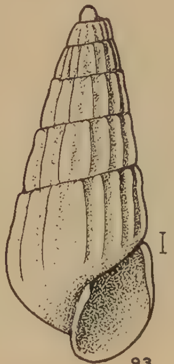
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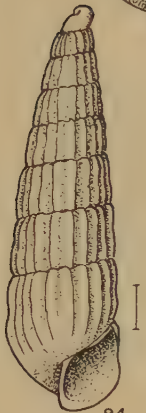
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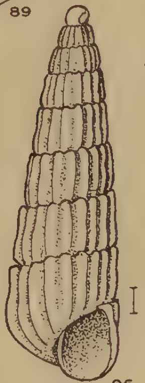
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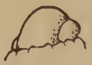
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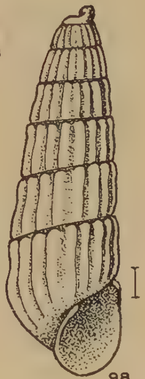
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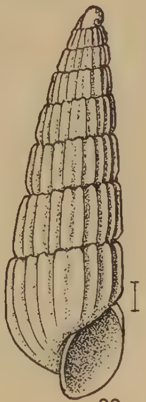
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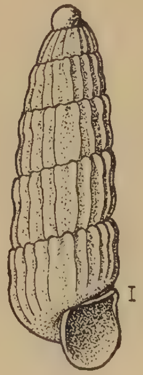
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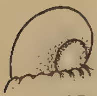
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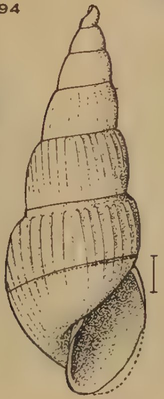
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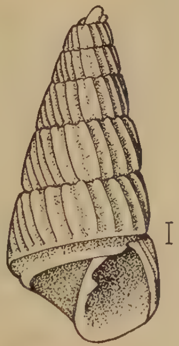
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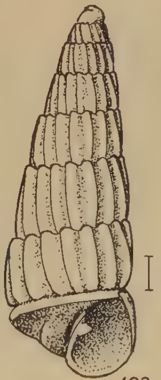
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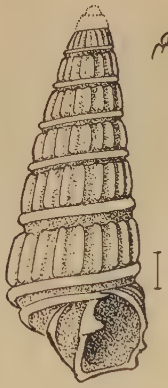
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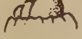
105

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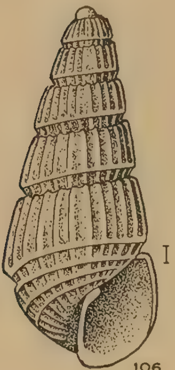
Fig. 89.—*Elodiamea iuga*, sp. nov., holotype. Fig. 90.—*E. proiectura*, sp. nov., holotype. Fig. 91.—*E. proiectura*, protoconch. Fig. 92.—*E. inverta*, sp. nov., holotype. Fig. 93.—*Exesilla conicera*, sp. nov., holotype. Fig. 94.—*E. sulcata*, sp. nov., holotype. Fig. 95.—*E. sulcata*, protoconch. Fig. 96.—*E. latacosta*, sp. nov., holotype. Fig. 97.—*E. latacosta*, protoconch. Figs. 98 and 99.—*E. latacosta*, variations. Fig. 100.—*E. nana*, sp. nov., holotype. Fig. 101.—*Tathrella iredalei*, sp. nov., holotype. Fig. 102.—*Paregila henni* (Brazier). Fig. 103.—*P. elongata*, sp. nov., holotype. Fig. 104.—*Babella caelata* (A. Adams). Fig. 105.—*B. caelata*, protoconch.



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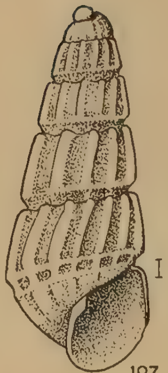

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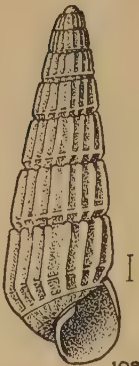

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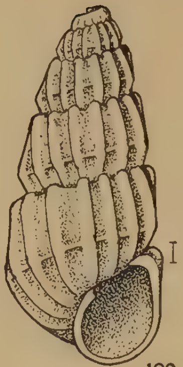

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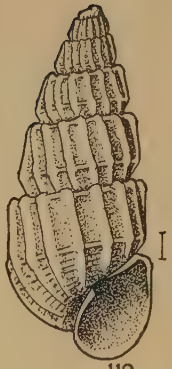

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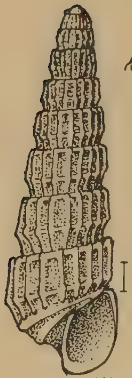

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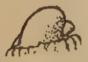

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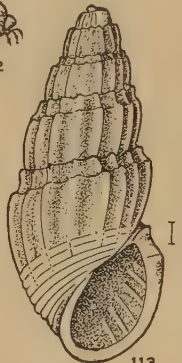

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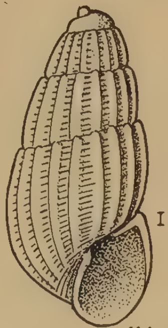

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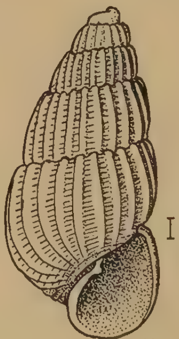

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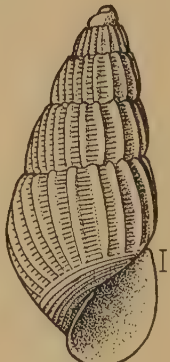

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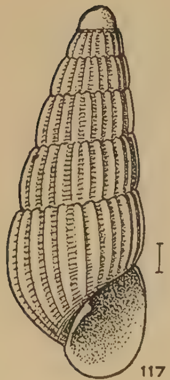

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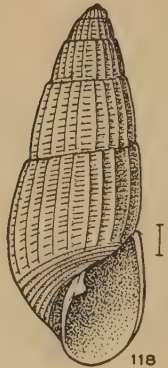

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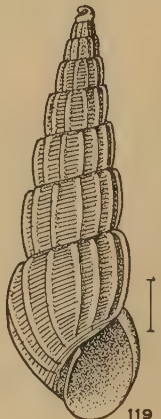

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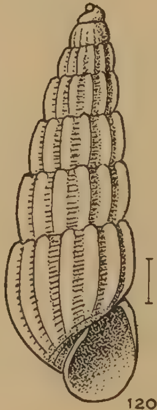

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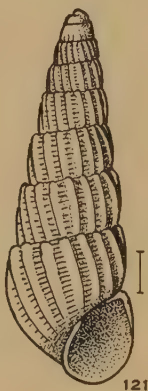

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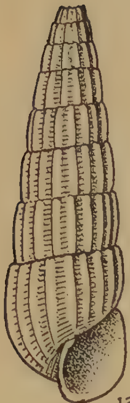
Fig. 106.—*Egila spiralis*, sp. nov., holotype. Fig. 107.—*E. typica*, sp. nov., holotype. Fig. 108.—*E. articulata* (Hedley), after Hedley. Fig. 109.—*E. univestis*, sp. nov., holotype. Fig. 110.—*E. curtisensis*, sp. nov., holotype. Fig. 111.—*E. australis*, sp. nov., holotype. Fig. 112.—*E. australis*, protoconch. Fig. 113.—*Eurathea humerica*, sp. nov., holotype. Fig. 114.—*Pyrgulina oodes* (Watson). Fig. 115.—*P. spissa*, sp. nov., holotype. Fig. 116.—*P. spissa*, variation. Fig. 117.—*P. affinis*, sp. nov., holotype. Fig. 118.—*Linopyrga maccullochi* (Hedley), after Hedley. Fig. 119.—*L. delicatula*, sp. nov., holotype. Fig. 120.—*L. oreades*, sp. nov., holotype. Fig. 121.—*L. declivita*, sp. nov., holotype.



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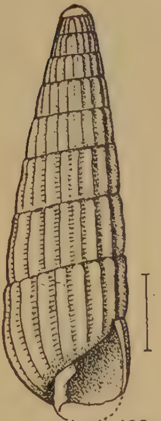

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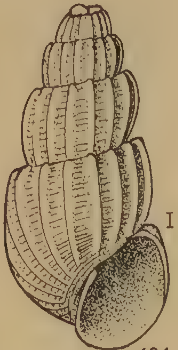

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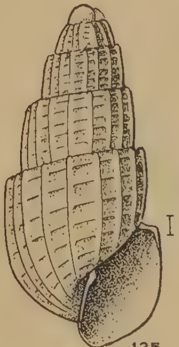

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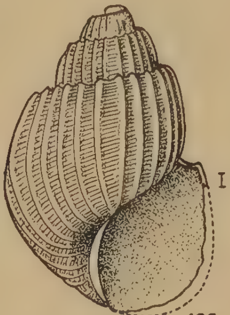

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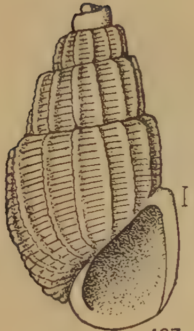

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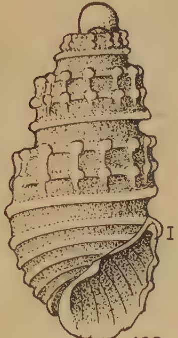

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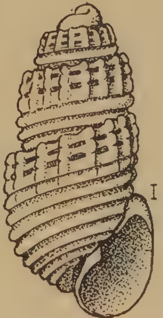

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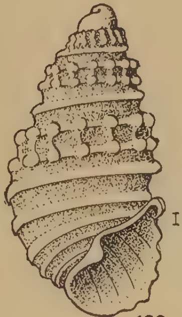

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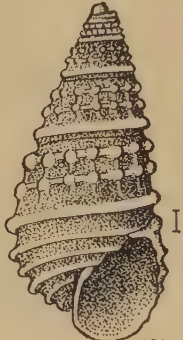

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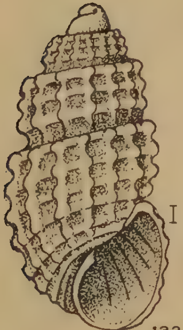

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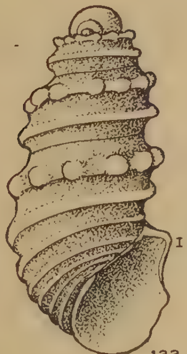

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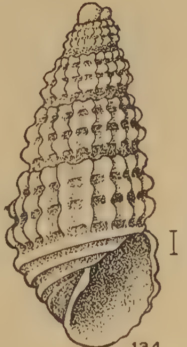

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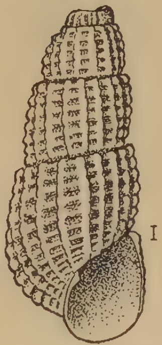

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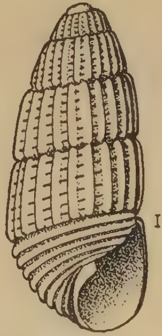

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Fig. 122.—*Linopyrga* sp. Fig. 123.—*L. incurva*, sp. nov., holotype. Fig. 124.—*L. perscalata* (Hedley). Fig. 125.—*L. reticulata*, sp. nov., holotype. Fig. 126.—*Quirella mirationis*, sp. nov., holotype. Fig. 127.—*Q. suprafila*, sp. nov., holotype. Fig. 128.—*Miralda senex* (Hedley), after Hedley. Fig. 129.—*M. senex*, variation. Fig. 130.—*M. umeralis* (Hedley), after Hedley. Fig. 131.—*M. conica*, sp. nov., holotype. Fig. 132.—*M. rugosa*, sp. nov., holotype. Fig. 133.—*M. revincta* (Hedley), after Hedley. Fig. 134.—*M. zea* (Hedley). Fig. 135.—*M. columna*, sp. nov., holotype. Fig. 136.—*M. tribulationis* (Hedley), after Hedley.

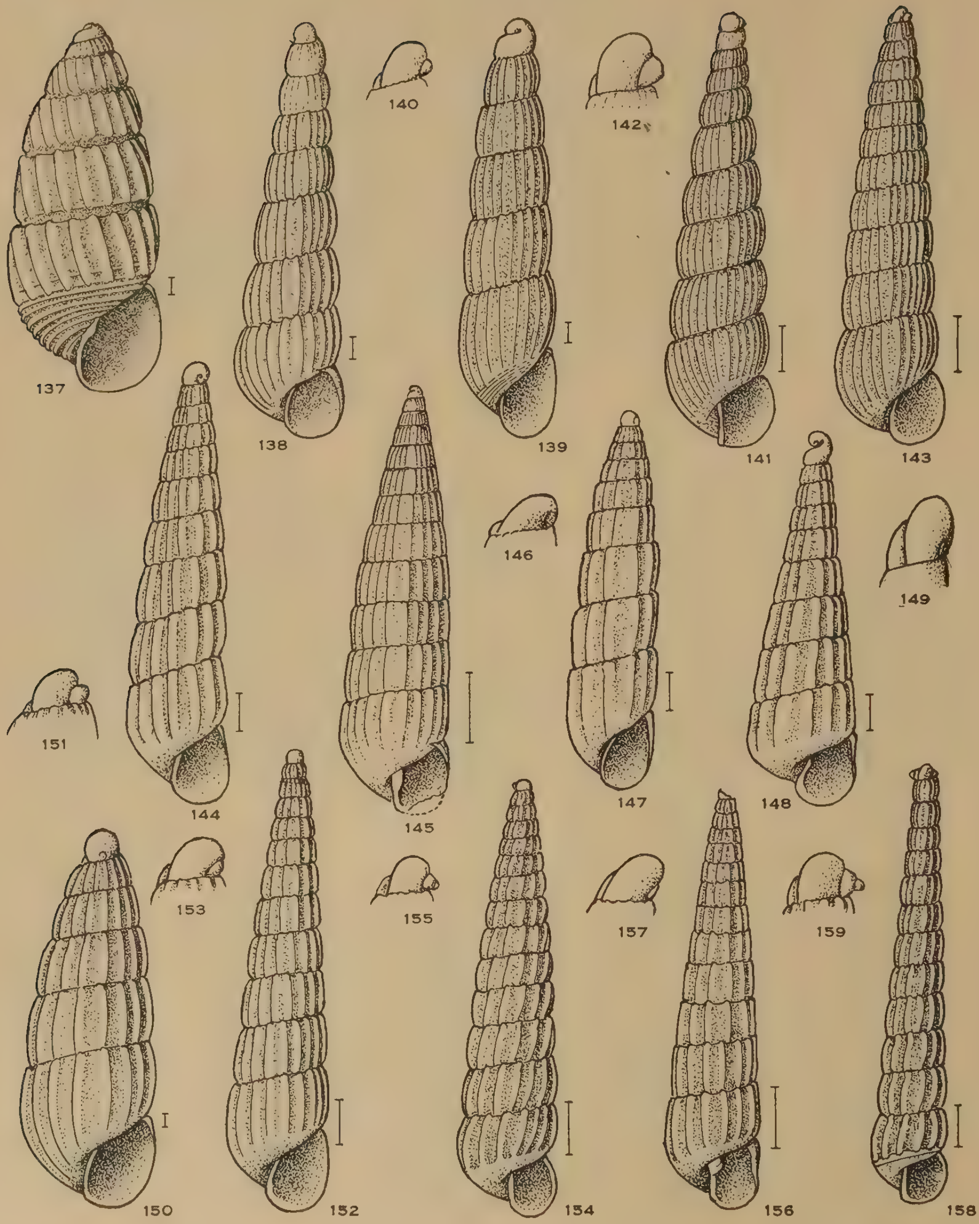

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Fig. 137.—*Miralda* sp. Fig. 138.—*Turbonilla tenuissima* Hedley. Fig. 139.—*T. darwinensis*, sp. nov., holotype. Fig. 140.—*T. darwinensis*, protoconch. Fig. 141.—*T. bowenensis*, sp. nov., holotype. Fig. 142.—*T. bowenensis*, protoconch. Fig. 143.—*T. ninona*, sp. nov., holotype. Fig. 144.—*T. vitrea*, sp. nov., holotype. Fig. 145.—*T. corrigea*, sp. nov., holotype. Fig. 146.—*T. corrigea*, protoconch. Fig. 147.—*T. paucina*, sp. nov., holotype. Fig. 148.—*T. conica*, sp. nov., holotype. Fig. 149.—*T. conica*, protoconch. Fig. 150.—*T. microscopica*, sp. nov., holotype. Fig. 151.—*T. microscopica*, protoconch. Fig. 152.—*T. felicita*, sp. nov., holotype. Fig. 153.—*T. felicita*, protoconch. Fig. 154.—*Chemnitzia darnleyensis* (Brazier), holotype. Fig. 155.—*C. darnleyensis*, protoconch. Fig. 156.—*Exesilla aplini* (Brazier), holotype. Fig. 157.—*E. aplini*, protoconch. Fig. 158.—*Chemnitzia gabrieli* (Hedley). Fig. 159.—*C. gabrieli*, protoconch.

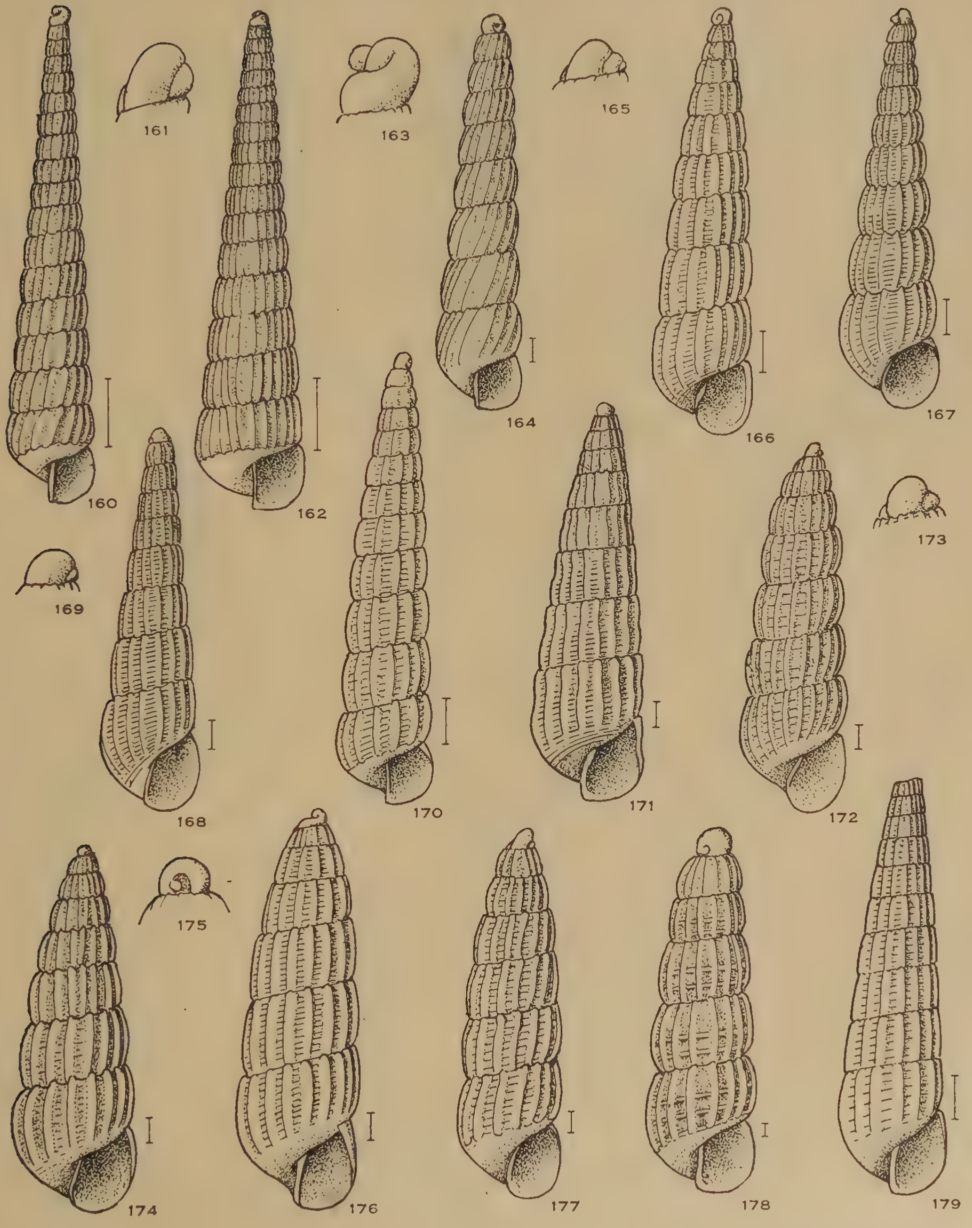

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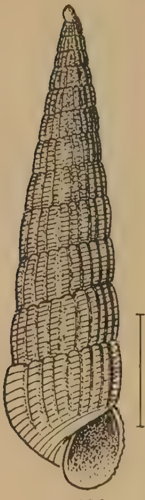
Fig. 160.—*Chemnitzia porrecta*, sp. nov., holotype. Fig. 161.—*C. porrecta*, protoconch. Fig. 162.—*C. queenslandica*, sp. nov., holotype. Fig. 163.—*C. queenslandica*, protoconch. Fig. 164.—*C. obliqua*, sp. nov., holotype. Fig. 165.—*C. obliqua*, protoconch. Fig. 166.—*Pyrgiscus confusus* (Brazier). Fig. 167.—*P. rhabdoides* (Watson). Fig. 168.—*P. rhabdoides*, variation. Fig. 169.—*P. rhabdoides*, protoconch. Fig. 170.—*Pyrgiscilla procerita*, sp. nov., holotype. Fig. 171.—*P. indenta*, sp. nov., holotype. Fig. 172.—*P. cheverti* (Hedley), holotype. Fig. 173.—*P. cheverti*, protoconch. Fig. 174.—*P. homoeatata* (Watson). Fig. 175.—*P. homoeatata*, protoconch. Fig. 176.—*P. homoeatata*, variation. Fig. 177.—*P. dipsycha* (Watson). Fig. 178.—*P. birestis*, sp. nov., holotype. Fig. 179.—*P. linearis*, sp. nov., holotype.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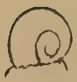
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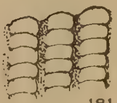
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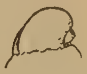
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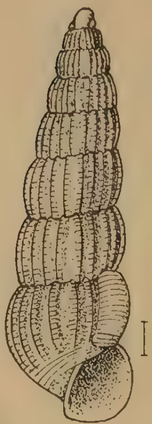
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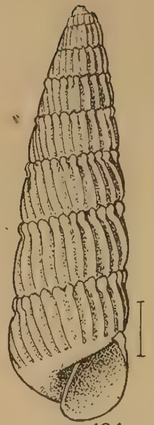
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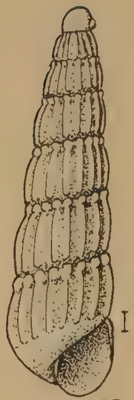
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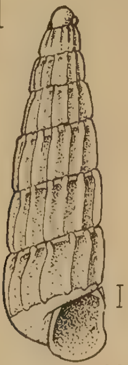
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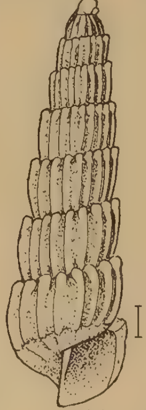
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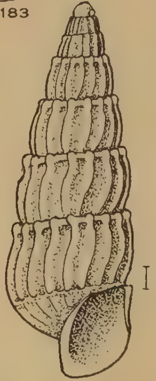
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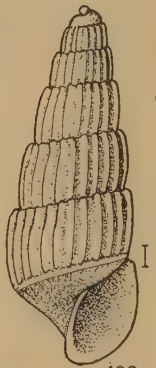
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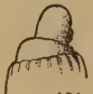
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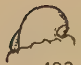
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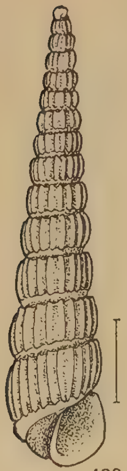
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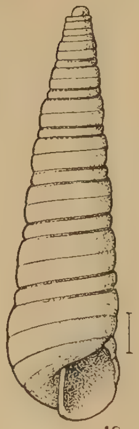
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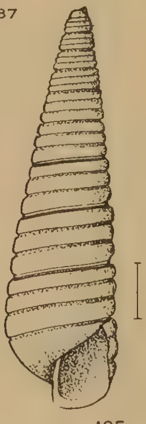
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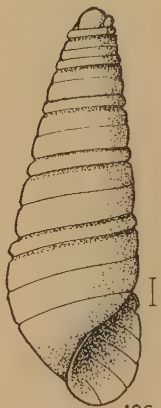
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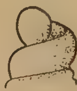
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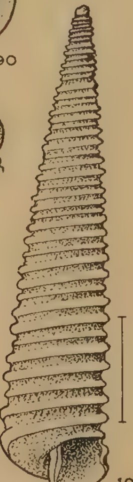
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Fig. 180.—*Mormulasta iredalei*, sp. nov., holotype. Fig. 181.—*M. iredalei*, sculpture further magnified. Fig. 182.—*M. iredalei*, protoconch. Fig. 183.—*Mormulasta* sp. Fig. 184.—*Zaphella nodulosa*, sp. nov., holotype. Fig. 185.—*Z. tropica*, sp. nov., holotype. Fig. 186.—*Z. subcarina*, sp. nov., holotype. Fig. 187.—*Z. tribulationis* (Hedley). Fig. 188.—*Z. tribulationis*, protoconch. Fig. 189.—*Z. tribulationis*, juvenile. Fig. 190.—*Z. vincula*, sp. nov., holotype. Fig. 191.—*Z. vincula*, protoconch. Fig. 192.—*Amamimormula torresiana*, sp. nov., holotype. Fig. 193.—*A. torresiana*, protoconch. Fig. 194.—*Cingulina austrina*, sp. nov., holotype. Fig. 195.—*C. austrina*, variation. Fig. 196.—*C. australis*, juvenile. Fig. 197.—*C. imperita*, sp. nov., holotype. Fig. 198.—*C. imperita*, protoconch.

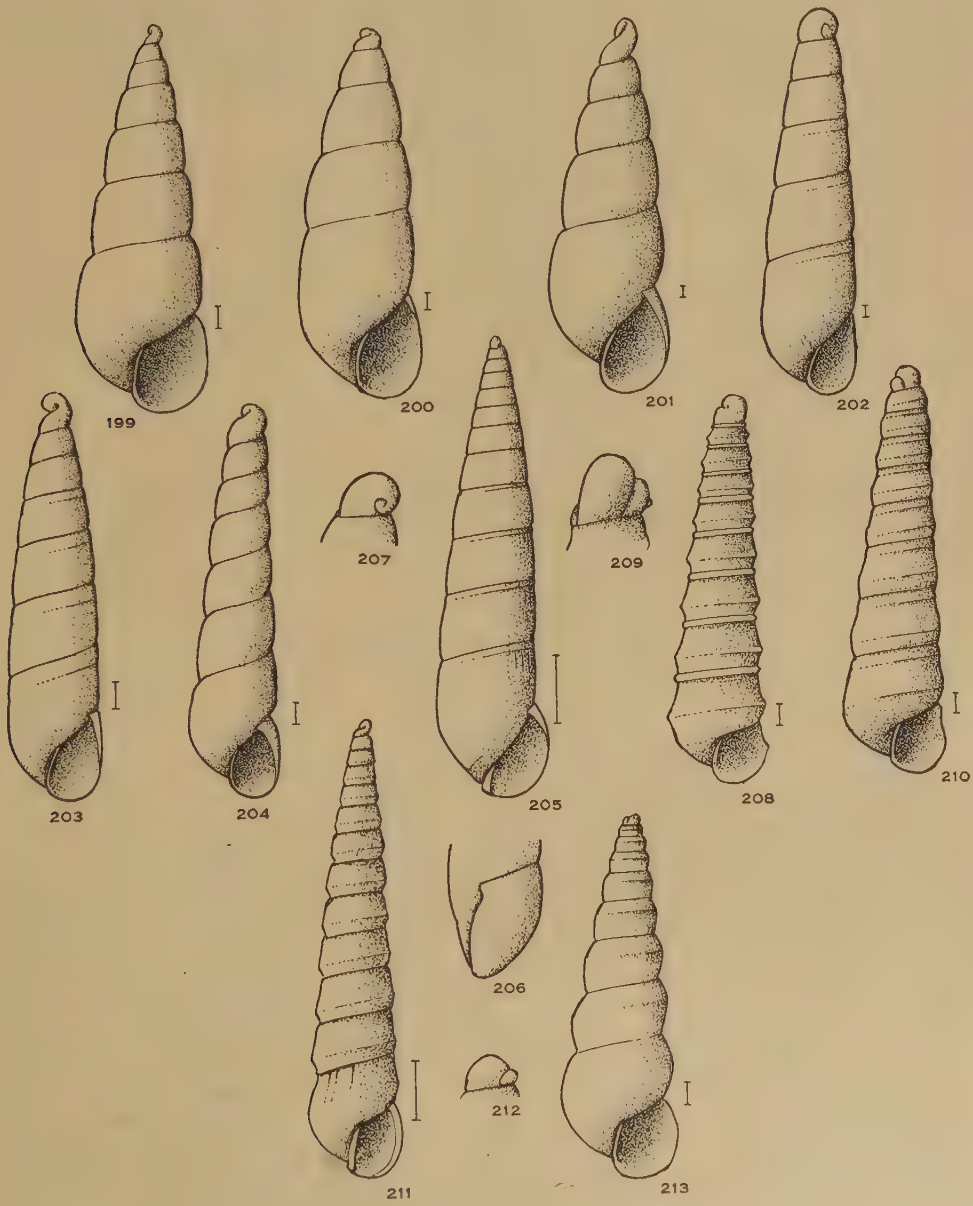

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Fig. 199.—*Koloonella capricornia*, sp. nov., holotype. Fig. 200.—*K. laxa* (Watson). Fig. 201.—*Koloonella* sp. Fig. 202.—*K. subtilis* (Watson). Fig. 203.—*K. subtilis*. variation. Fig. 204.—*K. tenuis*, sp. nov., holotype. Fig. 205.—*Paraloxella ambigua*, sp. nov., holotype. Fig. 206.—*P. ambigua*, lateral view of aperture. Fig. 207.—*P. ambigua*, protoconch. Fig. 208.—*Zonella amoebaea* (Watson). Fig. 209.—*Z. amoebaea*, protoconch. Fig. 210.—*Z. coacta* (Watson). Fig. 211.—*Instarella subcarina*, sp. nov., holotype. Fig. 212.—*I. subcarina*, protoconch. Fig. 213.—*I. subangulata*, sp. nov., holotype.

SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

I. GENERAL INTRODUCTION

By L. G. M. Baas Becking,*† J. M. Thomson,* and E. J. F. Wood*

[*Manuscript received February* 5, 1959]

Summary

In the period 1883–98 Lake Macquarie was the principal source of fish for Sydney and Newcastle. Since 1930 it has been only tenth or eleventh of New South Wales estuaries in fish production. The number of commercial fishermen in 1920 was 110, but today is only 35. Allegations of depletion prompted this investigation, the results of which are discussed in this series of papers.

Lake Macquarie is a coastal lake with a small freshwater inflow estimated to be only 4 per cent. of its volume. Attempts to improve the channel connecting the lake with the sea have failed repeatedly. A seemingly permanent result of the dredging is a great enlargement of the unproductive sand flat at the inner end of the channel. The soils of the lake's catchment area are poor in minerals. The land vegetation is mainly sclerophyllous forest with isolated patches of rain-forest and *Melaleuca* swamp.

The population has increased since the first settlement in 1825 until it is now over 50,000, but the lake is also a recreation area for the much larger population of Newcastle (over 200,000).

I. The Problem for Investigation

In 1953, following unusually emphatic allegations of depletion of the fish stocks in Lake Macquarie, the Division of Fisheries of the Commonwealth Scientific and Industrial Research Organization embarked upon a study of the fish and the related flora and fauna of Lake Macquarie to discover whether there had been a reduction of the fish population and, if so, whether this was due to overfishing or to some other cause.

It was beyond the resources of the Division to study the more difficult problems of the levels of production, or of energy levels, or of the total metabolism of the lake, which might have provided a sounder basis for the management of the fishery. Some aspects of the ecology which have a direct bearing on the defined object of the investigation were not studied; chief among these are the state of the invertebrate microfauna other than plankton, and the role played by birds. Further difficulties encountered were the lack of quantitative information on the immigration and emigration of fish, and the failure to obtain data on the impact of the sport fishery.

The papers which follow consist of independent reports on various ecological aspects of the biota and of the lake as an environment. The contribution of each

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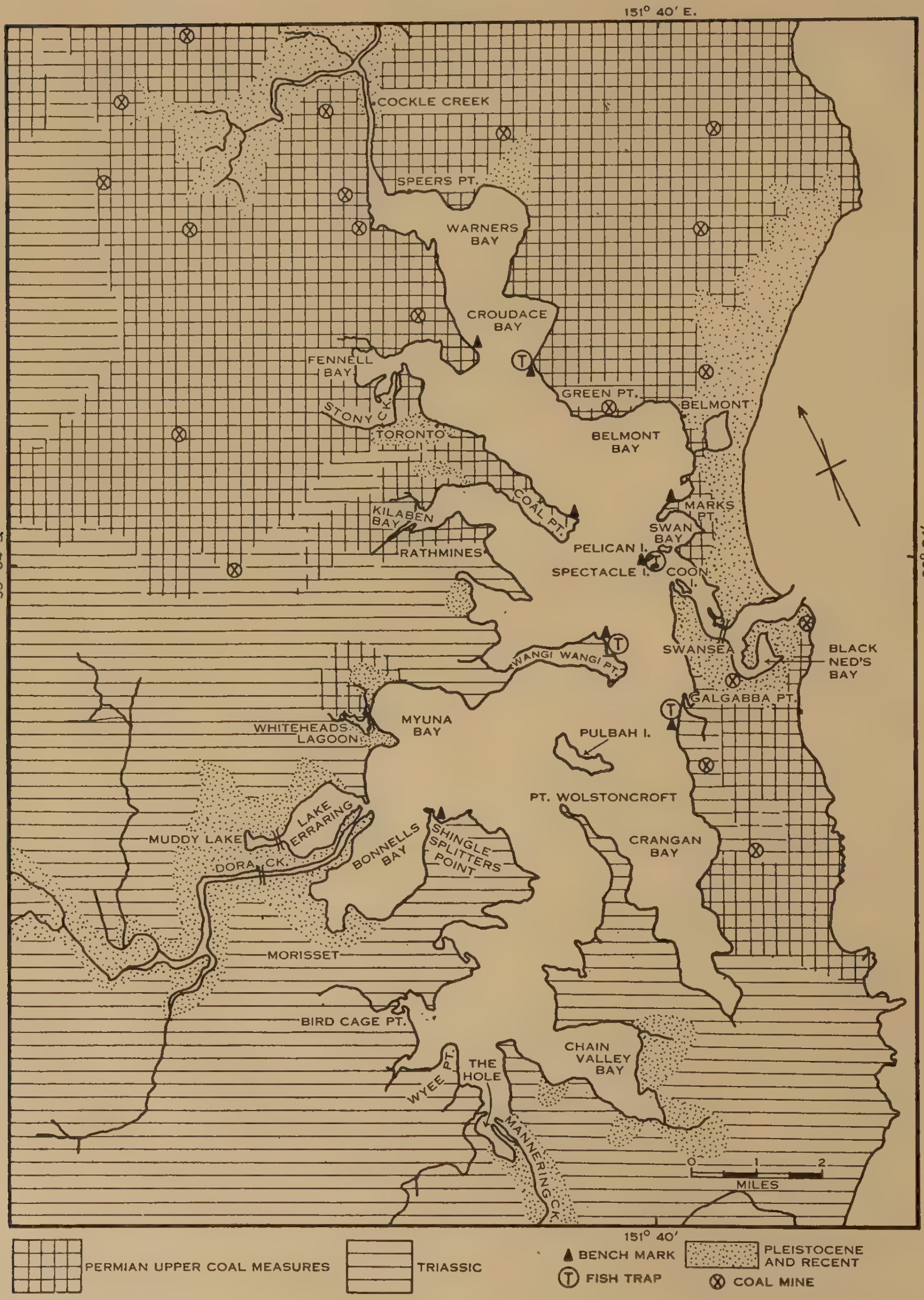
151° 40′ E.
COCKLE CREEK
SPEERS PT.
WARNERS BAY
CROUDACE BAY
FENNELL BAY
STONY CK.
TORONTO
GREEN PT.
BELMONT
BELMONT BAY
COAL PT.
KILABEN BAY
RATHMINES
MARKS PT.
SWAN BAY
PELICAN I.
SPECTACLE I.
COON I.
33° 04′ S.
33° 04′
SWANSEA
BLACK NED'S BAY
WANGI WANGI PT.
GALGABBA PT.
WHITEHEADS LAGOON
MYUNA BAY
PULBAH I.
PT. WOLSTONCROFT
LAKE ERRARING
MUDDY LAKE
DORA CK.
BONNELLS BAY
SHINGLE SPLITTERS POINT
CRANGAN BAY
MORISSET
BIRD CAGE PT.
CHAIN VALLEY BAY
WYEE PT.
THE HOLE
MANNERING CK.
0 1 2
MILES
151° 40′
PERMIAN UPPER COAL MEASURES
TRIASSIC
BENCH MARK
FISH TRAP
PLEISTOCENE AND RECENT
COAL MINE

Fig. 1.—Lake Macquarie, showing places mentioned in the text, the site of the fish traps and the bench marks, and the geological nature of the terrestrial environment.

paper to the main objective of the investigation is reviewed in the final summarizing paper to develop logically a coherent theory consistent with the observed facts.

This introductory paper describes the general topography of the lake and the general nature of the terrestrial environment around its shores. It gives a sketch of the history of the fishery.

II. Topography of the Lake

(a) *The Lake Basin and its Catchment Area*

Lake Macquarie, lying immediately south of the city of Newcastle on the east coast of Australia, was formed since the last Ice Age by the incursion of the sea into a valley among the coastal hills. The original entrance to this drowned valley was once much wider but is now filled in by sand deposition stretching for 2 miles between the townships of Swansea and Belmont (Fig. 1).

The outline of the lake is very irregular; the lake has a foreshore of about 365 miles, but an area of only a little more than 42 square miles. The greatest length from north to south (Cockle Creek to Chain Valley Bay) is 13 miles; the maximum width from west to east (Dora Creek to Galgabba Point) is 5·5 miles. The lake is divided naturally into two portions by the projection of Wangi Wangi Point. This division is rendered still more effective by the wide extension of sandy shallows from the eastern shore opposite this point so that the only deep-water connection between the two parts of the lake is by a narrow channel close alongside the point. The channel itself is interrupted by submerged ridges which break the continuity of the deeper water layers.

The maximum depth recorded during these investigations was 51 ft between Pulbah Island and Galgabba Point. Apart from this hole the floor of the lake is rather flat and averages about 22 ft.

The watershed of Lake Macquarie (calculated from the Army Ordnance map of 1941) is between 150 and 160 square miles. Apart from the areas of Pleistocene and Recent deposits (Fig. 1) the surrounding country is hilly, over half the catchment area being above 22 ft above lake level, with hills rising to 1400 ft in the north-west section of the catchment. There are no major rivers entering Lake Macquarie. The chief contributors to the run-off are Mannering Creek in the south, Cockle Creek in the north, and Dora Creek in the west. The other creeks are small and contribute little to the total run-off. All the creeks are evanescent and flow only during rainy periods. The average annual rainfall, calculated from records (30-year period) for Wyee and Cockle Creek, is 42·28 in.

(b) *The Entrance Channel*

The entrance is roughly L-shaped (Fig. 2). From the lake the channel runs almost southwards for 8000 ft; there it turns towards the east to cover the same distance to the end of the breakwaters which enclose the entrance. The configuration of the channel has been changed from time to time by dredging and the building of training walls. The history of these changes can be followed in a series of 17 maps (Appendix I, Table 2) which date from 1826 to 1954. Supplementary information is contained in documents on file with the Harbours and Rivers Branch of the New South Wales Department of Public Works, and in the Mitchell Library, Sydney (Appendix II).

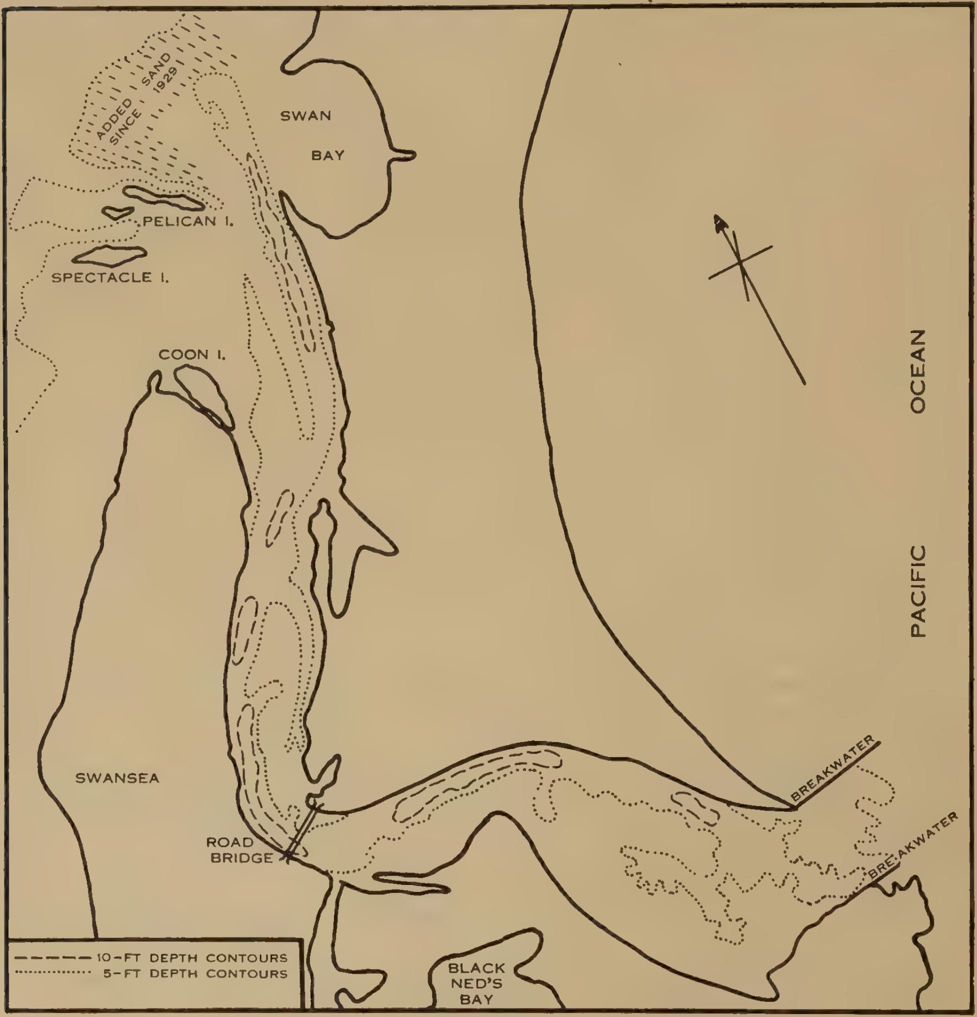
SAND ADDED SINCE 1929
SWAN BAY
PELICAN I.
SPECTACLE I.
COON I.
SWANSEA
ROAD BRIDGE
BREAKWATER
BREAKWATER
PACIFIC OCEAN
BLACK NED'S BAY
10-FT DEPTH CONTOURS
5-FT DEPTH CONTOURS

Fig. 2.—The entrance channel to Lake Macquarie.

Map 3 (Appendix I) shows that the natural channel meandered in 1841. The first attempt to control the channel was made in 1864 when dredging was done near Pelican Island, and stoneworks were commenced on the northern side of the channel in the lower section running east and west. These works were not effective, or were not completed, for in 1874, when further works were in progress, it was reported that part of the earlier retaining wall had been unearthed. In 1883 work was started on the retaining wall on the northern side of the channel, and in 1884 breakwaters, 1400 ft apart, were built at the mouth of the channel. Up to this time it had been possible to ford the channel by means of a sand spit not far from the mouth (Jervis 1945).

In 1896 a newspaper report (*Sydney Morning Herald*, January 29, 1896) commented upon the bad state of the channel. As early as 1887 Sir John Coode, an expert engineer, had commented adversely upon the channel works, and had estimated that to maintain sufficient scour to keep the channel free from siltation, the distance between the breakwaters should be no more than 200 ft. This expert advice does not appear to have been followed and the continual dredging necessary to keep open the wider channel appears to have been beyond the capacity of the available dredging plant. For many years no dredging took place, and it was renewed only when public demand became great.

TABLE 1

HISTORY OF CHANGES IN THE CHARACTERISTICS OF THE ENTRANCE CHANNEL

A, Above bridge; *B*, below bridge (Fig. 2)

Characteristic	1861	1879	1887	1908	1914	1921	1929	1954
Area (10^6 sq. ft)								
A		10·80			12·90		17·04	17·65
B		7·53			11·10			7·15
Total		18·33			24·00			24·70
Deeper than 5 ft, *A*	3·31	2·32	2·36	3·42	3·91		4·35	4·83
Deeper than 5 ft, *B*	1·83	1·81	1·82		3·44	2·74	3·19	4·44
Deeper than 5 ft, total	5·14	4·13	4·18		7·35		7·54	9·27
Deeper than 10 ft, *A*	0·33	0·10	0·26		0·88		1·40	0·62
Deeper than 10 ft, *B*	0·16	0·17	0·20		1·07		0·57	0·51
Deeper than 10 ft, total	0·49	0·27	0·46		1·95		1·97	1·13
Volume (10^7 cu. ft)								
A		3·19			5·01		6·54	5·39
B		2·81			4·31		3·77	4·40
Total		6·00			9·32		10·31	9·79
Length of channel (ft)								
Deeper than 5 ft	18600	18300	16000		19600		17500	18300
Deeper than 10 ft	3280	1500	4500		9000		11300	
Area of sand wedge (10^6 sq. ft)	5·14*			7·66			7·78	10·10

* In 1864.

The early charts show the natural channel flowing south of Pelican Island, but the dredged channel was cut north of the island. When dredging ceased in 1944 the artificial channel was obliterated and the natural channel has gradually re-established itself. What is now generally called Pelican Island originated in sand dumped by the dredgers at the beginning of the century and the present Spectacle Island is the original Pelican Island. This can be shown by measuring on successive charts the distance of the island from the extreme tip of Coon Island, which was originally Point Keep Clear.

The chief change in the entrance (Table 1) during the last century has been the pushing-out of the sand bank at the inner end of the entrance channel to increase the shallows in that region. The early charts show that sand bars have always been present at both ends of the entrance channel. Even when dredging was being carried out the channel through the inner bar was only a little wider than two boat widths. The entrance is clearly delimited from the deeper waters of the lake by a steep sandy slope. From the early charts the area of the entrance channel, including the shallows at the lakeward end, may be calculated as 0·60 square miles, but during this investigation it was estimated to be 0·89 square miles. The increase is due to the great development of the sandy shallows which increased by 5×10^6 sq. ft between 1861 and 1954. In the aerial survey photographs of 1941 (Appendix I, Map 16), these shallows appear as a wedge of sand encroaching into the lake. The wedge is fan-shaped and shallow, with a few poorly defined channels forming a kind of inverted delta. The sand spit at the seaward end of the entrance is slowly re-establishing itself. Considerable areas of these more recently formed sand flats are devoid of plant and animal life.

III. Terrestrial Environment

(a) *Geology*

David (1950) considered this area briefly, and roughly mapped the geological structure. The southern and south-western part of the lake is on Triassic sandstone with some alluvium around the creeks. The north-western, north-eastern, and south-eastern parts are Permian and belong to the Newcastle series of the Upper Coal Measures. In the Swansea–Belmont region these coal measures are covered with Pleistocene and Recent sand; windblown sand occurs between Swansea and Redhead. The coal measures at the northern end of the lake are interrupted only by some post-Tertiary alluvium near Cockle Creek and a few minor creeks and by a Triassic intrusion westward at Wangi. There are more than 20 coalmines, most of them in operation, in the immediate vicinity of the lake. Both main geological formations yield poor yellowish to greyish podzolic soils, often in thin layers. After abortive attempts, grazing, dairying, and the raising of grains have been given up, except on the alluvial flats, because of the nature of the soil. The low mineral content of the run-off water would be expected to influence the ecology of the lake.

(b) *Vegetation*

The quality of the soil also determines the type of plant communities around the shores of the lake. This shore vegetation is, apart from mangrove, *Avicennia officinalis*, chiefly of the dry sclerophyll type, with the following exceptions: (1) remnants of rain-forest on the east scarp of the divides; (2) remnants of a *Livingstonia–Macrozamia* assembly between Swansea and Mark's Point merging towards the east into a swamp community with *Melaleuca viridiflora* and *Eucalyptus robusta*; (3) a small assembly of *Banksia serratifolia* and *Leptospermum laevigatum* on a

Permian intrusion north of Dora Creek. Dr. E. Hotchkiss (personal communication) has listed 106 higher plants including 11 exotics from Point Wolstoncroft. Most of the Lake Macquarie watershed consists of cut-over secondary sclerophyll forest.

IV. History of the Fishery

The lake was discovered in 1800, when Captain William Reed in the *Martha* mistook the entrance for that of the Hunter River. Early settlement was sparse until the development of the area when the Sydney–Newcastle railroad was opened in 1889. By 1911 the population of Lake Macquarie Shire was less than 8000, but 54,000 is the estimated figure for 1959 (Anon. 1950). The northern foreshores of the lake are now largely suburbs of Newcastle or tourist centres carrying large summer populations. Much of the southern foreshores is still bushland or very sparsely populated.

Although fishing to fulfil local needs must have started much earlier it was not until 1863 that fish from Lake Macquarie was sent to Newcastle and Sydney markets (Anon. 1874). By 1883 Lake Macquarie had become the principal source of supply for the Sydney and Newcastle fish markets, according to the Report of the New South Wales Fisheries Commissioners for 1883. The fish had to be transported by a rough road 12 miles to Newcastle where it was placed on a coastal steamer for Sydney. Because no ice or other form of refrigeration was available the transport by road took place by night to lessen the likelihood of fish spoilage.

The shallow bar prevented direct shipments from the lake but in 1886 arrangements were made for a small boat from the lake to ferry the fish catch to the Newcastle–Sydney steamer standing by outside the entrance. However, this scheme failed owing to lack of support from the fishermen themselves (see the Fisheries Commissioners report for 1886).

In 1889 the railway from Newcastle to Sydney opened and the portion of the catch destined for Sydney was thenceforward sent by train, mostly from Dora Creek. Prior to this time a considerable proportion of the catch had been smoked or otherwise preserved, but subsequently the curing trade declined.

Except for 1894 when it came second, Lake Macquarie remained the most productive of New South Wales fishing areas until 1898 when the provision of better transport opened up both the north and south coasts. However, it remained as one of the first six until after 1930 when it dropped to tenth or eleventh.

During the period 1886–1910 the number of professional fishermen working on the lake averaged about 80 but during the period of 1913–20 more than 110 men were fishing. In the twenties, a sharp decline brought the number to an average of 60 which continued to the outbreak of war in 1939. From 1939 to 1945 an average of 42 men fished the lake. Since then a further decline to less than 35 fishermen has been brought about by the law of 1947 which restricted the issue of licences to full-time fishermen. These figures refer to annual averages. In any particular month the number of fishermen working on the lake may be higher owing to the temporary influx of fishermen licensed in other districts, or lower because local fishermen have followed good fishing elsewhere or are having their annual lay-up period.

It is impossible to estimate the number of anglers. The lake is only a few miles from the industrial centre of Newcastle and is also a tourist resort, with a much augmented population during the summer months, particularly from January to April. As a result the angling body is drawn from a much wider group than the 50,000 or so residents of Lake Macquarie Shire.

V. ACKNOWLEDGMENTS

The assistance and cooperation of the Superintendent of Fisheries of New South Wales, who supplied unpublished data on the fishery and made the services of his officers available, and of the Fisheries Inspectors responsible for the supervision of Lake Macquarie are gratefully acknowledged. The Trustees of the Mitchell Library kindly gave access to a number of historical documents dealing with Lake Macquarie.

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APPENDIX I

MAPS OF LAKE MACQUARIE

TABLE 2

LIST OF MAPS

No.	Date	Surveyor	Area and Scale	Source
1	1826	Finch	Lake	(4)*
2	1829	Ralphe	Lake	(6)
	1830			(8)
3	1841	W. S. Proctor	Eastern part only, 1 mile/1 in. Insert: Lake, 10 miles/1 in.	Mitchell Library F14/67
4	May 1861	A. Rossbach	Entrance, Lake head to ocean, 300 ft/1 in.	†
5	Sept. 1864	E. Forde	No. I. Entrance to Kahibah. No. II. Kahibah to Pelican. 300 ft/1 in.	†
6	Aug. 1879	T. Eccles	Entrance, total 300 ft/1 in.	†
7	1887	Sir John Coode	Entrance, total 300 ft/1 in.	†
8	Sept. 1908	Anon.	Lake head to Kahibah, 300 ft/1 in.	†
9	1911 (1937)	J. Marshall P. Higgins	Lake, ½ mile/1 in. Soundings on same map	†
10	Sept. 1914	S. R. Mallarky	Entrance, total 300 ft/1 in.	†
11	Sept. 1921	H. H. Kelly	Entrance to bridge, 300 ft/1 in.	†
12	July 1929	E. D. Cowdery	Entrance, total 300 ft/1 in.	†
13	1941	D. R. B. Portus	Lake head to bridge, 300 ft/1 in.	†
14	1939	E. M. Beach	Centre of Lake, 8 miles/1 in. Insert: locality Rathmines, ¼ mile/1 in.	†
15	1941	2nd Field Survey Ord. Co., R.A.A.	1 mile/1 in.	Army
16	1950 1952	R.A.A.F.	Air Survey, entire lake, 300 ft/1 in.	R.A.A.F.
17	June–July 1954	E. M. Beach	Entrance, total 300 ft/1 in.	†

* Refers to publications listed in Appendix II.

† Harbours and Rivers Branch, Public Works Department, New South Wales.

Appendix II

LITERATURE CONSULTED ON THE HISTORY OF LAKE MACQUARIE

(Nearly all of this material obtained through the kindness of the Mitchell Library)

(1) *The Australian*, February 4, 1841, p.2.

(2) *The Australian*, May 13, 1841, p.2.

(3) Boon, L., in *Newcastle Herald*, December 6, 1952.

(4) Clout, N. M. The Child of Bahtahbah. Paper read before the Newcastle and Hunter River Section of the Australian Historical Society, March 27, 1947.

(5) Coode, Sir John. "Lake Macquarie Harbour Works." (Govt. Printer: Sydney.)

(6) Governor's Dispatches, New South Wales, 1833, No. 23, p.474 and p.1212.

(7) Huntington, H. W. H. History of Newcastle and the Newcastle District. (Newspaper clippings, undated, possibly 1885 to 1890.)

(8) Jervis, J. J. Lake Macquarie, its discovery and settlement. *J. Roy. Hist. Soc.* **31**: 101–25.

(9) *Maitland Mercury*, November 23, 1861.

(10) Anon. (1950). "The Newcastle Region. A Preliminary Survey of the Resources." (Govt. Printer: Sydney.)

(11) New South Wales Calendar and Directory, 1833.

(12) Oliver, A. (1893). "A History of Fisheries in New South Wales." (Govt. Printer: Sydney.) (Prepared for the Chicago Exposition of 1893.)

(13) Oyster beds at Lake Macquarie. Unsigned and undated MS. in Mitchell Library. Apparently *c.* 1885.

(14) Plimmer, J. (1893). Pleasure Resorts of New South Wales.

(15) *Sydney Morning Herald*, August 3, 1840.

(16) *Sydney Morning Herald*, September 10, 1841.

(17) *Sydney Morning Herald*, October 2, 1841.

(18) *Sydney Morning Herald*, June 17, 1864.

(19) *Sydney Morning Herald*, January 29, 1896.

(20) *Sydney Gazette*, September 17, 1827.

(21) Tenison-Woods, J. E. (1882). "Fish and Fisheries in New South Wales." (Govt. Printer: Sydney.)

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(23) "Tourist Guide to the Hawkesbury and the Lake Macquarie Region, 1889." (Govt. Printer: Sydney.)

(24) "Tourist Handbook North Coast and Lake District, 1909." (Govt. Printer: Sydney.)

(25) *Town and Country Journal*, November 21, 1874.

(26) *Town and Country Journal*, March 3, 1886.

SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

II. HYDROLOGY

By R. S. Spencer*

[*Manuscript received February* 5, 1959]

Summary

Lake Macquarie is a marine-dominated drowned valley connected to the sea by a shallow narrow channel which damps tidal oscillations from 5 ft on the coast outside to about 3 in. in the lake. Superimposed on the semi-diurnal tides are changes in level in response to changes both in the external daily mean sea-level and in the volume of fresh water discharge into the lake.

Temperature and chlorinity cycles are closely linked. Discharge from the creeks supplies phosphate but little nitrate for the lake. Prolonged heavy rainfall in both 1955 and 1956 produced stratification of the water associated with lowered oxygen tension in the underlying salt water. There is evidence of a wind-generated circulation within the lake.

I. Introduction

During the course of the hydrological investigations at Lake Macquarie, which extended over three years (1954 to 1956), it became apparent that because of the very poor development of tidal circulation, the system would be greatly affected by freshwater discharge. It was decided to examine in some detail the response of various hydrological properties to such discharge, and in addition the factors influencing changes in lake level and internal circulation. Conditions favourable to the development of stratification were brought about in the autumn of 1955 and 1956 by abnormally high rainfall, and a comparison could be made between these years and 1954, when the marine domination of the system was in evidence.

II. Methods

(*a*) *Chlorinity*

In the early stages of these investigations chlorinity was determined by the Knudsen titration method. Subsequently a portable chlorinity–temperature meter (Hamon 1956) was used and thus vertical profiles of chlorinity, with readings at metre intervals from surface to bottom, were obtained in a few minutes. Where samples were collected with Nansen bottles for other analyses, chlorinity was determined in the laboratory with the meter.

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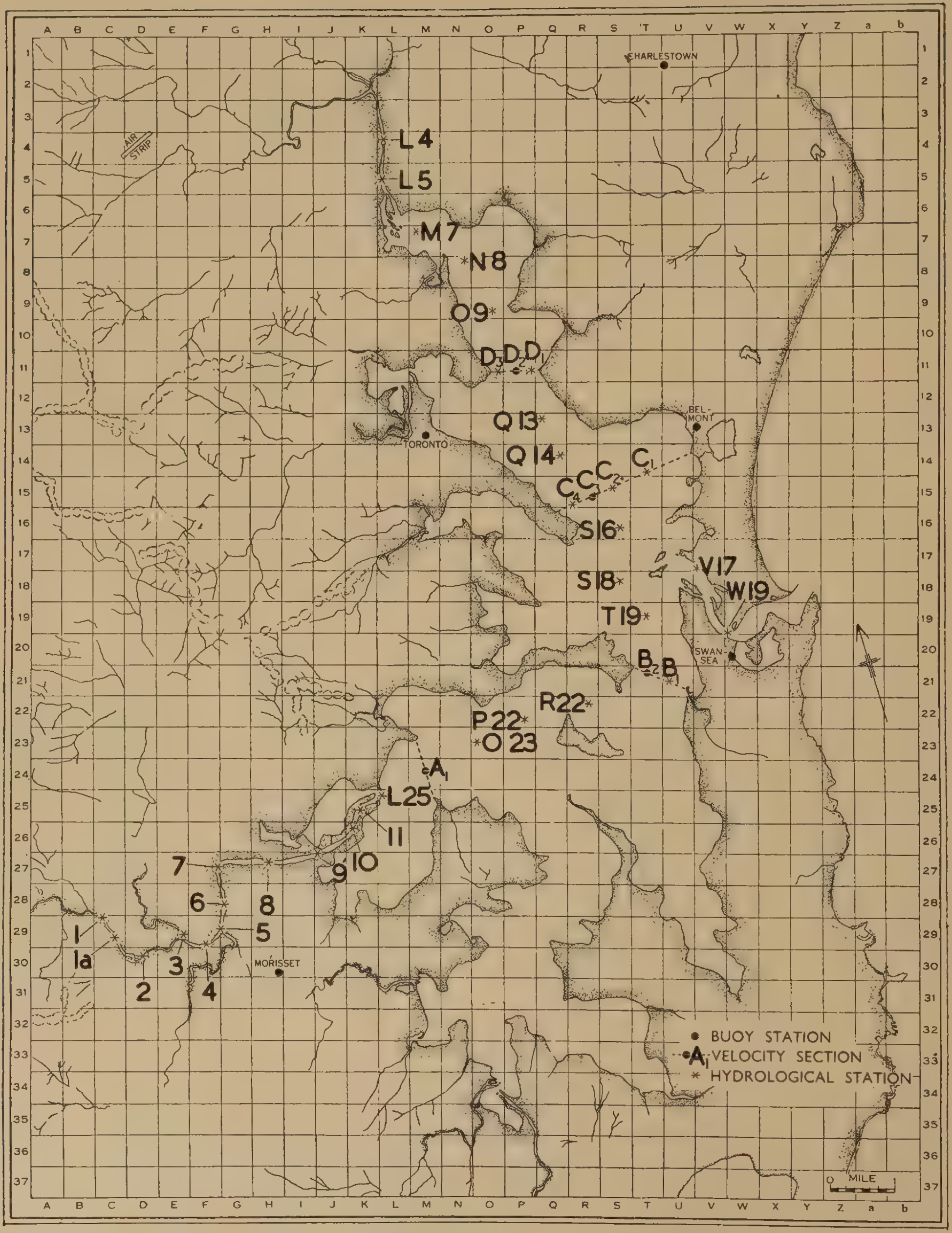
CHARLESTOWN
AIR STRIP
L4
L5
M7
N8
O9
D3 D2 D1
Q13
TORONTO
BEL-MONT
Q14
C4 C3 C2 C1
S16
V17
S18
W19
T19
SWAN-SEA
B2 B1
R22
P22
O23
A1
L25
11
10
9
7
6
8
5
1
1a
3
2
4
MORISSET
BUOY STATION
A1 VELOCITY SECTION
HYDROLOGICAL STATION
0 MILE 1

Fig. 1.—Grid map of Lake Macquarie. Stations not specifically marked are located by grid reference.

(*b*) *Temperature*

Where the chlorinity–temperature meter was used in the field to determine chlorinity, a reading of temperature *in situ* was also made. Before this instrument was developed all temperatures were recorded with a reversing thermometer attached to a Nansen bottle.

(*c*) *Dissolved Oxygen*

The standard Winkler method in conjunction with the tables of Fox (1907) was used to determine dissolved oxygen.

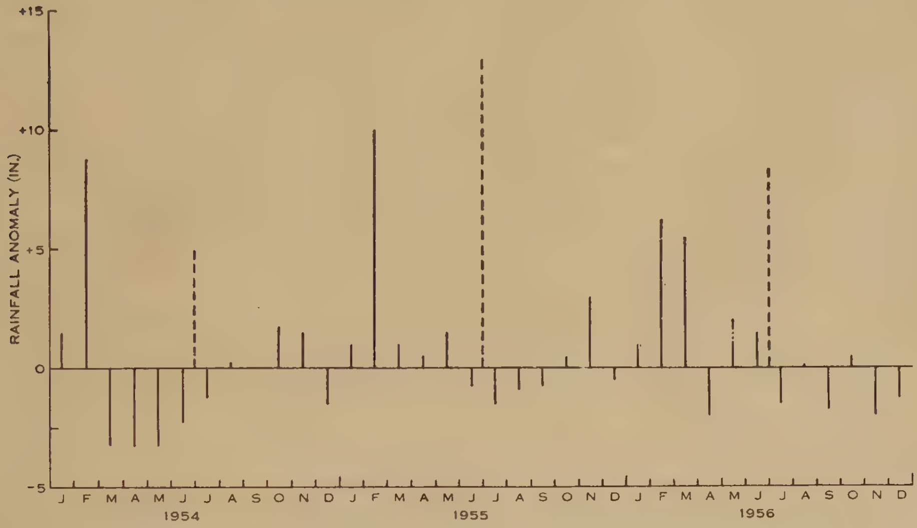

Fig. 2.—Monthly and annual rainfall anomalies in the Hunter River district, 1954–56. ———Monthly anomalies; – – – – – –annual anomalies.

(*d*) *Nitrate*

The reduced strychnine reagent described by Rochford (1947) was used to determine nitrate. The values have been recorded as μg nitrate nitrogen per litre.

(*e*) *Phosphate*

Two phosphate fractions (inorganic and soluble organic) were determined on each sample. The methods were those described by Rochford (1951), and the values have been recorded as μg phosphorus per litre.

(*f*) *Current Velocity*

Observations on current velocity were made in the Swansea channel with a Price current meter.

The data used in this paper have been published (C.S.I.R.O. Aust. 1956, 1957*a*, 1957*b*). The stations mentioned in the text are shown in Figure 1.

III. Rainfall

Figure 2 shows the monthly rainfall anomalies in inches during the period 1954–56 in the Hunter district, which includes Lake Macquarie and its drainage system. The annual rainfall, shown by broken lines, was above average in each year, but its monthly distribution was a vitally important factor in the observed hydrological cycles.

Rainfall of flood proportions occurred in February (late summer) of each year; however, the subsequent autumn patterns were quite different. In 1954 this latter period was one of drought, so that the flood discharge was not maintained, and therefore had little influence on the normal marine dominations of the system. The following year can be described as the "most violent" because of a maximum positive anomaly in February which caused a considerable discharge of freshwater into the lake. In 1956 the rainfall was again above average in February, though not as high as the previous year; however, there followed a further positive anomaly in March, as a result of which the subsequent stratification was more prolonged than in 1955.

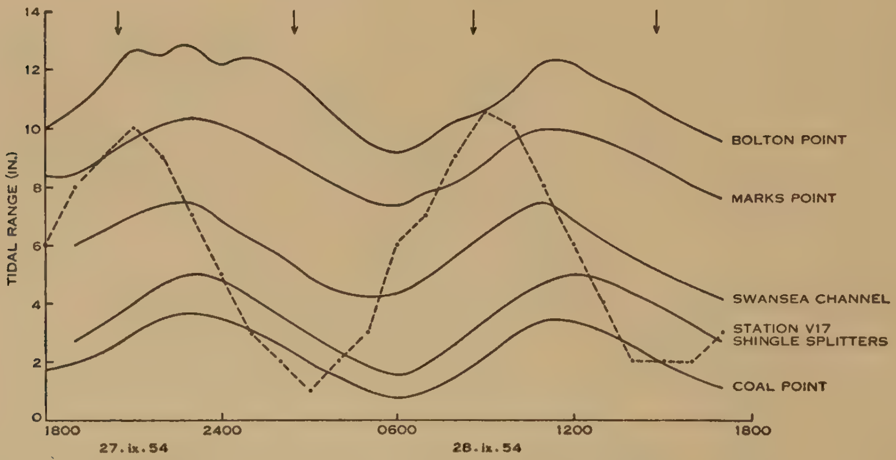

Fig. 3.—Simultaneous recordings of water level at selected bench marks, 27–28.ix.54. Arrows show times of high and low water at the Fort Denison tide gauge.

IV. Tidal Characteristics and Level Changes

The narrow winding Swansea channel, which connects the lake to the sea, is so effective in damping out the semidiurnal tidal variations that the amplitude is reduced from some 5 ft at the entrance to about 3 in. within the lake itself. Figure 3 shows the results of simultaneous readings of water level made at selected bench marks over the lake. Except for Station V17, which is in the Swansea channel, all observation points show a tidal range of about 3 in., with high and low water occurring simultaneously; the tidal lag compared with the outside sea is about 3 hours.

Velocities within the channel reach several knots in the region of the bridge. The period of slack water is extremely brief, and the period of maximum velocities corresponds in time to high or low water. This fact is not unusual when one considers that the channel is not estuarine, but simply a narrow connection between two comparatively large and deep bodies of water.

During the early stages of these investigations an attempt was made to determine the volume of water transported through a cross section of the channel on an average tide. The main area of this cross section, at Station V17, was estimated at 10^4 sq. ft, and hourly velocity readings were made at the surface and 4 m from a jetty at the shore. Periodic measurements were made at points across this section, and compared with those at the jetty. Within the limits of accuracy of the total transport measurement, the velocities at any time can be considered similar throughout the section. Figure 4 shows the velocity curve obtained during such a survey.

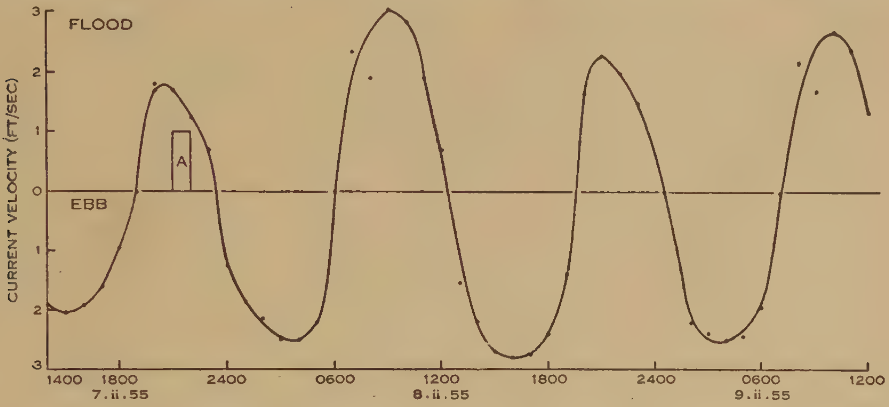

Fig. 4.—Tidal curve of current velocity at Station V17, 7–9.ii.55.

The area within rectangle *A* shown in Figure 4 represents a flow of 1 ft/sec for 1 hour, or $3 \cdot 6 \times 10^3$ cu. ft through a cross-sectional area of 1 sq. ft. The total flow through the whole section is therefore $3 \cdot 6 \times 10^7 \times N$ cu. ft, where N is the number of rectangles within each tidal curve.

Current measurements over a period of 6 months, during which time about 30 tidal curves were obtained, showed a range of values for N from 5 to 15, so that the transport volume is of the order of 10^8 cu. ft. This represents about 1 per cent. of the total volume of the lake.

The accuracy of the order of magnitude of this volume estimation can be roughly checked by calculating its effect on the water level of the lake. As stated previously the average depth is 21 ft, so that the expected tidal elevation should be 2–3 in.; this agrees with observed values.

As a minimum the lake could be completely ventilated by 100 tidal cycles, if the entire volume entering on each tidal cycle were retained within the lake.

That this is not so was shown in both 1955 and 1956. The volume of marine water gained by the system on each tidal cycle must be considerably less than the observed transport volumes.

To investigate tidal cycles within the lake a recorder was installed at Mark's Point (see Fig. 1). Weekly charts were obtained which recorded the actual magnitude of level changes without any reduction in scale.

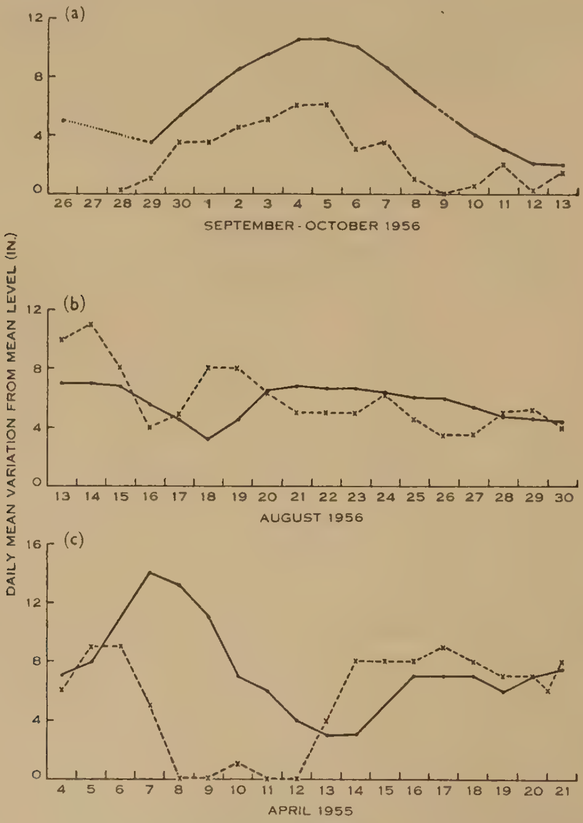

Fig. 5.—Comparison between changes in mean lake level and mean sea-level, derived from records at Port Hacking: (*a*) steady sea-level change, (*b*) rapid external fluctuation, (*c*) addition of freshwater to lake. ————Mark's Point recorder; – – – – – –Port Hacking.

It soon became evident that changes in lake level were being superimposed on the actual semi-diurnal tidal fluctuation. In Figure 5 these changes have been compared with simultaneous changes in external mean sea-level, calculated from tidal records obtained at Port Hacking. Generally speaking the relationship between the two was not constant.

If mean sea-level changes steadily over a period of several days the lake level follows the same pattern. The change should be in the same direction, up or down, but rapid mean sea-level fluctuations of small amplitude are not reflected in the lake (Fig. 5(*a*)).

Rapid fluctuations of greater amplitude produce a more complicated picture. Such rapid external fluctuations are shown in Figure 5(*b*), and there appears to be a time lag of about 2 days before such fluctuations are reflected in a change in lake level. The duration and magnitude of mean sea-level changes therefore control the variations in mean lake level.

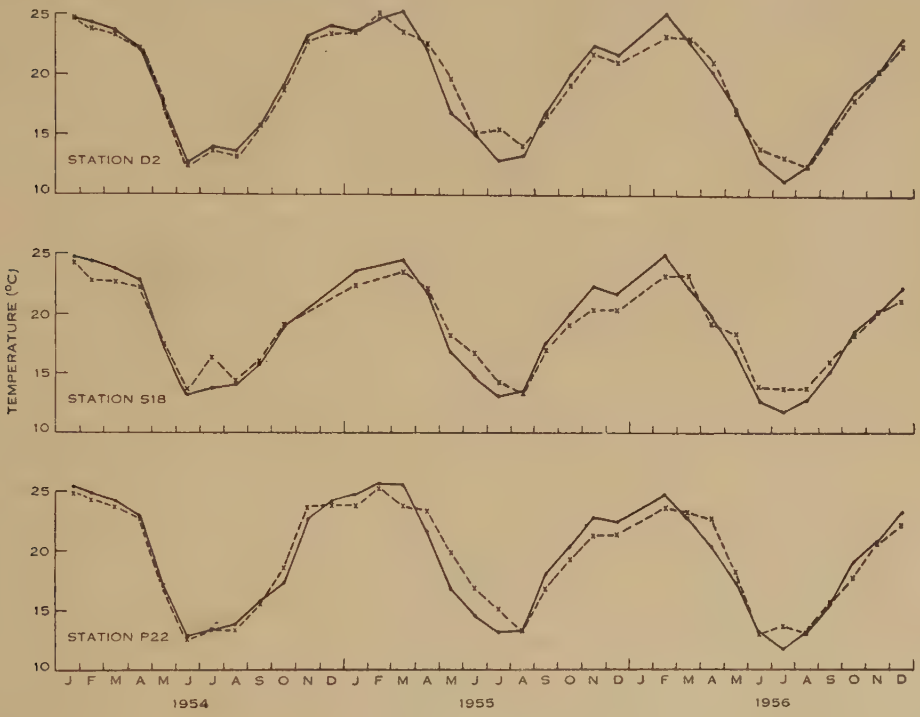

Fig. 6.—Seasonal cycles of temperature in the northern, central, and south-western regions of Lake Macquarie over three years, 1954–56. ———— Surface observations; – – – – – – bottom observations.

The addition of freshwater to the lake by rainfall discharge introduces a further complicating factor, the effect of which depends on the mean sea-level changes occurring at the time. In Figure 5(*c*), for example, the lake level was elevated initially by rainfall discharge, and maintained for several days despite a very considerable fall in mean sea-level. When the external level was kept low for several days the lake ultimately responded in the usual way, and a considerable discharge must have occurred through the Swansea channel. Had the rather exceptional fall in mean sea-level not occurred the hydrostatic head within the lake, produced by rainfall discharge, would no doubt have maintained high lake levels for a greater period of time than was actually the case.

V. Temperature and Chlorinity

Observations made on these two properties show that they are so closely linked that they should be discussed in a single section. Figures 6 and 7 show the seasonal cycles of temperature and chlorinity during the period 1954–56 at three selected stations, which can be considered representative of conditions in the northern (Station D_2), central (Station S18), and south-western (Station P22) regions of the lake. Horizontal gradients in both properties are only slight at the surface except under conditions of flood discharge. This latter factor, which was observed in the later summer of 1955 and 1956, greatly influences the subsequent vertical temperature gradients.

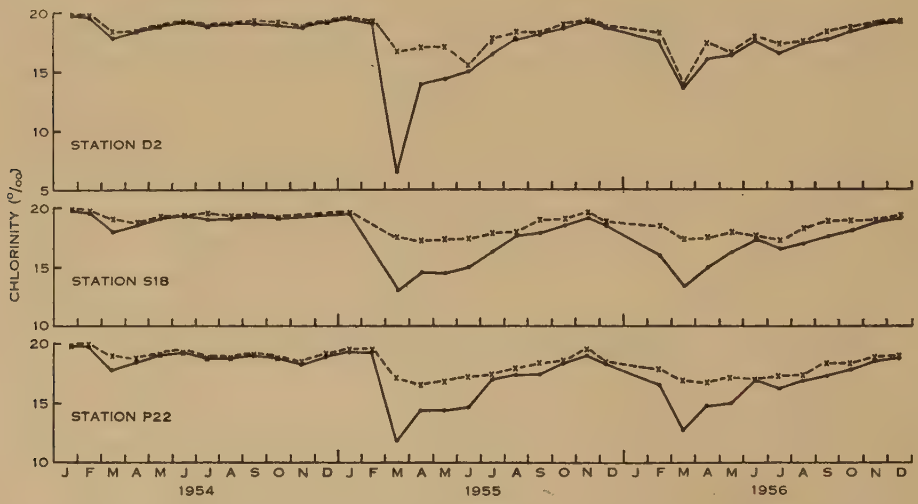

Fig. 7.—Seasonal cycles of chlorinity in the northern, central, and south-western regions of Lake Macquarie over three years, 1954–56. ———— Surface observations; – – –×– – – bottom observations.

In the autumn–winter period of 1954, when vertical chlorinity gradients were negligible (Fig. 7), the seasonal loss of heat was virtually constant throughout the entire water column at each of the three selected stations. The high temperature recorded at Station S18 in July of this year was due to the intrusion of marine water. This vertical homogeneity extended over the spring period as well.

In February 1955 rainfall was extremely high (see Fig. 2), and considerable dilution of surface waters was observed in the following month. The associated stratification persisted throughout the cooling period, and as a result the vertical temperature gradients were considerably higher than in the corresponding period of 1954. This effect was most marked at Station P22; as this station is more remote from the channel entrance, its bottom waters are more likely to remain isolated.

Although the vertical chlorinity gradients were quite small during the spring of 1955, they were apparently sufficient to develop decreasing thermal gradients, much greater than anything observed in 1954.

Further abnormal rainfall early in 1956 produced stratification once again, although it was not so intense as in the previous year (see Section III). The same may be said for the vertical temperature gradients during the cooling period; once again Station P22 showed the maximum effect. During the spring of this year chlorinity gradients persisted, but the preferential heating of the surface waters was far less obvious than in 1955.

Marine water, which enters the central lake region through the Swansea channel, has a more restricted temperature range than the lake water, and should therefore exert a warming or cooling effect, depending on the season of the year. This effect has frequently been observed during the period of investigation. Figure 8 shows the movement of marine water up the channel on a flood tide in June 1956, and its subsequent replacement by the discharge of lake water. The temperature–chlorinity properties of each component are clearly differentiated; the incoming marine water had a temperature of 17·5°C and a chlorinity of 19·4‰, whereas the lake water had a temperature of 13·5°C and a chlorinity of 16·7‰. It is of some interest to note here that, except for the initial stage of the ebb cycle, homogeneous conditions prevailed throughout, the water column consisting entirely of marine or lake water. On the flood cycle the pressure of incoming marine water was sufficient to force all the lake water out of the channel, leaving a homogeneous marine column; on the other hand, once the ebb phase was well developed, the surface lake water, which within the lake itself occupied a depth exceeding that of the upper channel, occupied the entire water column at the observation point.

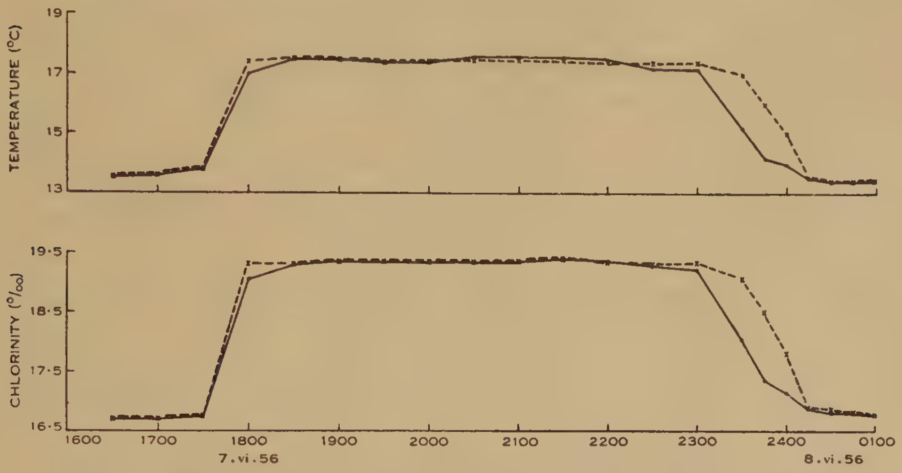

Fig. 8.—A tidal curve of chlorinity and temperature at Station V17, 7–8.vi.56.
————Surface observations; – – – – – –bottom observations.

The marked differences in the composition of those two components led to an investigation of the fate of the marine component once it entered the lake proper. Figure 9 shows the changes which occurred in the chlorinity and temperature profiles in a section from the "dropover" to a point about 300 yd west, on the morning following the previous survey. Three such profiles were observed over a period of about 90 min, each run occupying about 5 min; values of chlorinity and temperatures were read at metre intervals at the stations shown.

In the first profile the flood cycle was just commencing; the chlorinity–temperature characteristics of the lake water are the same as those shown in Figure 8. In the second profile the intrusion of marine water had produced considerable density gradients, where previously there had been an almost homogeneous water column. By the time the third profile was completed the flood strength had apparently been reduced, as the lake water was now closer to the dropover. Vertical gradients were now greater at the outer station, as the marine water spread further into the lake.

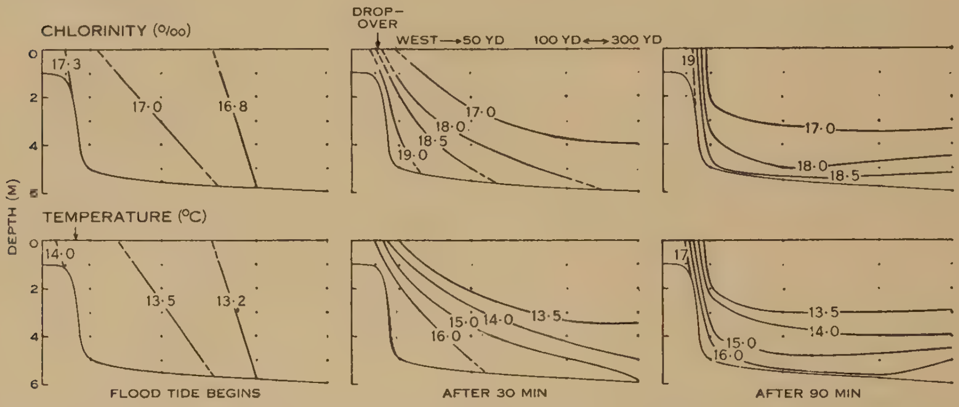

Fig. 9.—The movement of marine water across the Swansea channel dropover, and its effect on the temperature–chlorinity structure of this area.

Two days previously, the changes in the structure of the water column at Station C_3 had been examined over a tidal cycle. These changes are shown in Figure 10, with local high and low water marked on the time scale. The effect of high-temperature, high-chlorinity water entering on the flood cycle is obvious; this water disappeared during the ebb phase, but was detected again in the later stages. However, the chlorinity profiles showed different characteristics on each occasion. During the flood cycle a homogeneous layer developed above the boundary, as the rate of transfer of water across this boundary exceeded its subsequent removal. This effect has been observed and discussed at some length by Tully (1949). When the boundary reappeared during the ebb phase the rate of transfer apparently equalled the rate of removal, as a linear gradient was observed above the boundary. It seems likely that the changes in the velocities of the two components (surface lake water and marine water) were responsible for these different profiles.

The effect of marine water intrusion appears to be rapidly damped out at greater distances from the channel entrance. Figure 11 shows the changes that occurred in the chlorinity structure at Station B_2 later in June 1956. Some oscillations were observed, but they could not be related to the tidal phase. They probably represent the effect of internal waves of comparatively long period, induced by the rapid changes in structure near the dropover.

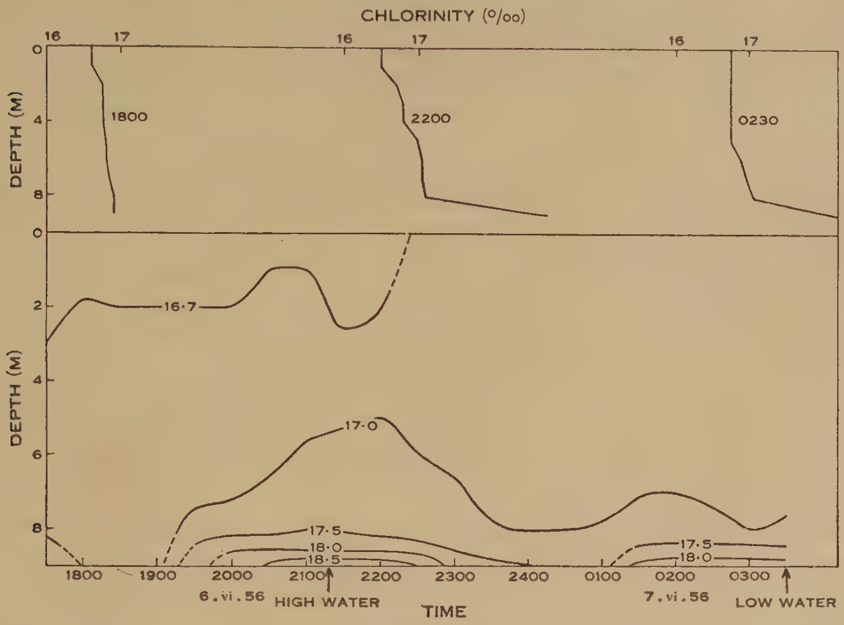

Fig. 10.—Tidal profile of chlorinity at Station C_3, 6–7.vi.56, with chlorinity–depth curves at selected stages of the tidal cycle.

The use of the chlorinity–temperature meter during 1956 gave a clearer understanding of the relationships existing in Lake Macquarie. These relationships for selected months are shown in Figure 12. In February the mixing line was inclined to the left at an angle of about 45° from the vertical (its position in midsummer under drought conditions). Rainfall discharge into the system at this time was

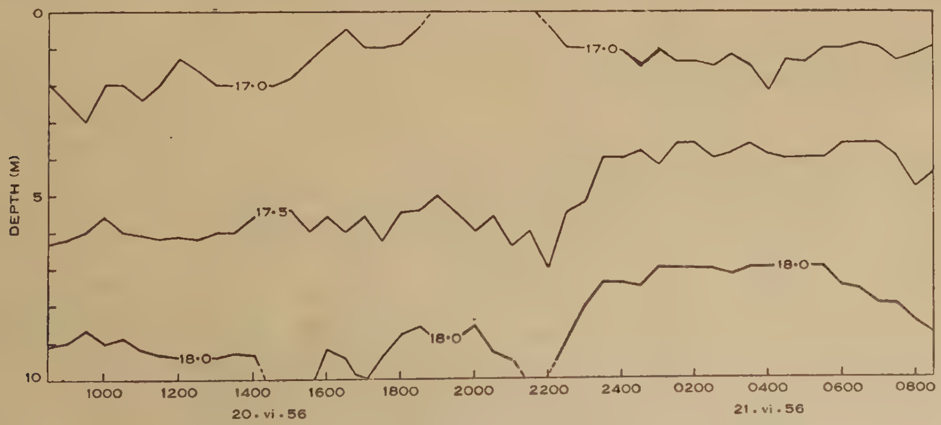

Fig. 11.—Tidal profile of chlorinity at Station B_2, 20–21.vi.56.

rapidly incorporated into the surface waters of the lake. In March the seasonal heat loss was becoming apparent, but the extensive discharge, which had been maintained since the February survey, produced a considerable spread of points about the expected horizontal line.

In April the mixing line had reversed in the south-west region, owing to a considerable cooling at the surface which was not reflected in the bottom waters.

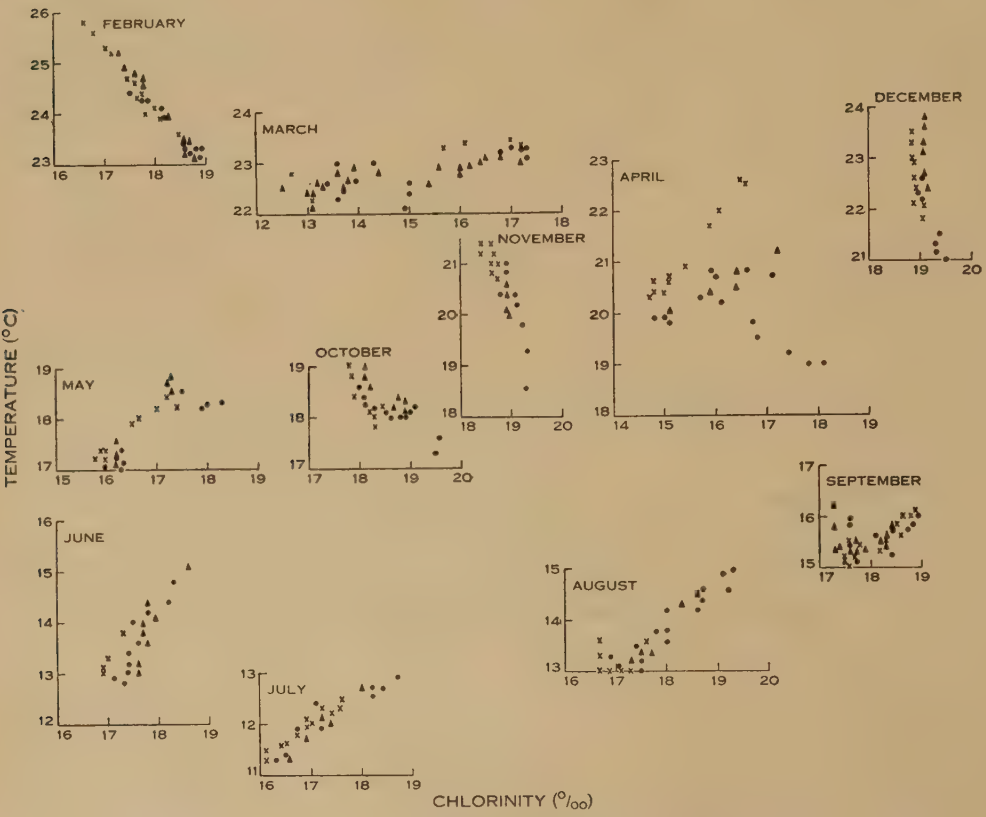

Fig. 12.—Chlorinity–temperature relationships in Lake Macquarie during 1956. ×, Northern region; ●, central region; ▲, south-western region.

The number of significant observations in the northern region is scarcely sufficient to be conclusive, but the points suggest the same pattern as in the south-western region. In the central region the mixing line is distinctly curved, owing to the intrusion of low temperature marine water, which was obviously having a profound effect on the chlorinity–temperature properties of the bottom waters in this region.

During the ensuing month the loss of heat from the system proceeded at a rapid rate, so much so that in May the mixing line had passed that expected in a stratified system. By July the winter state had been reached, and was maintained even into September. Subsequently the homothermal state was reached and passed as vernal heating occurred. By this time the chlorinity gradients were greatly reduced, and in the south-western region the mixing line was very close to the expected vertical. In the central and northern regions, however, the influence of marine water was apparent. By the end of the year all three mixing lines were vertical, and the chlorinity was virtually uniform except for the bottom waters in the immediate vicinity of the dropover.

VI. Wind-Generated Circulation

Since wind energy was considered important in the formation of the homogeneous layer of surface lake water, its effect on the depth of this layer was examined in 1956. Figure 13 shows two density distributions along the north-south axis of the lake, the first following a period of fresh southerly winds, lasting several days, and the second 2 days later. During the period between the two sections very light northerly winds prevailed.

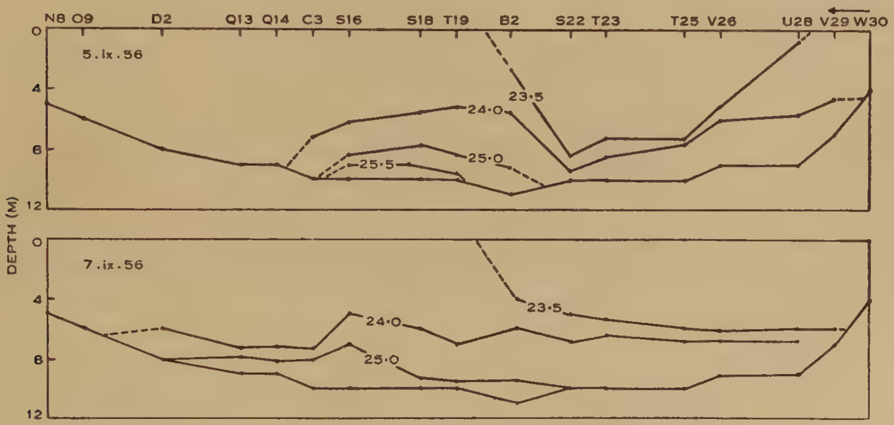

Fig. 13.—Effect of wind changes on density sections along the north–south axis of Lake Macquarie.

The results show that for the purpose of this discussion the north-south axis of the lake can be divided into two regions. The extensive shallows to the east of Station B_2 cause an effective restriction in the width of the lake. As a result low density water was piled up against this bank to the south of Station B_2, with an upwelling of high density water further south. In the northern region of the lake there was a considerable piling-up of surface water, its density being slightly higher than that in the south.

The removal of the wind-energy source produced marked changes in density distribution; once again the two regions mentioned above appeared to respond separately. In the north the front of bottom water was observed to move approximately 2 miles in the interval between sections.

The density distribution in the central lake on the first section suggests a greater influence of marine water. This may be so, but both sections were completed in about 3 hours during a flood tide. Nevertheless, even allowing for this fact the movement of the bottom zone into the northern region of the lake can hardly be doubted, as it has been observed on a number of occasions. Ultimately the density distribution could be predicted before a section was carried out, by referring to the preceding wind patterns.

This type of change in density distribution, which is a comparatively slow one, obviously complicates the interpretation of oscillations such as those shown in Figure 11.

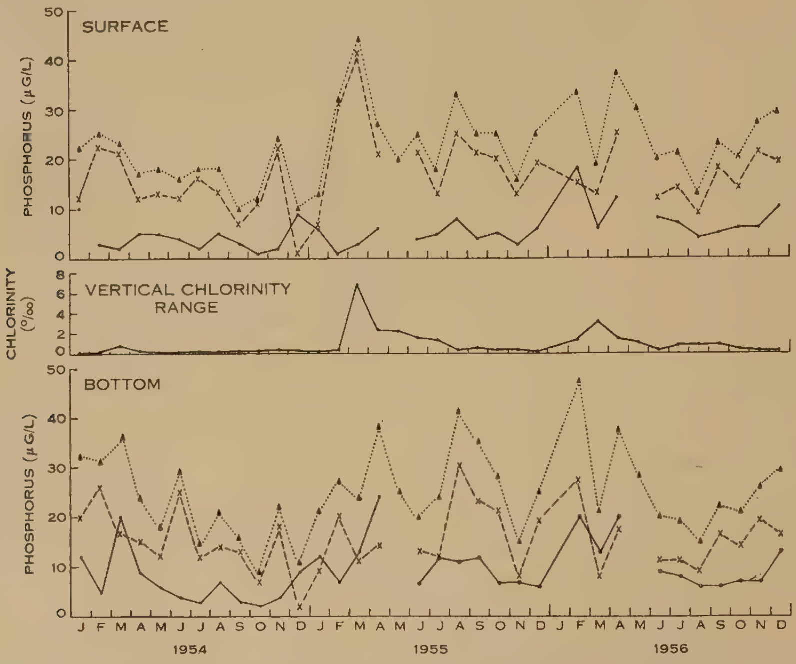

Fig. 14.—Seasonal cycles of inorganic and organic phosphate in Lake Macquarie, 1954–56, together with the vertical chlorinity range. The points shown represent the mean of seven lake stations (A_1, P22, B_2, S18, C_3, D_2, and N8). ———— Inorganic P; ×– – – –× organic P; ▲......▲ total P.

VII. Nutrient Cycles

(a) *Phosphate*

Figure 14 shows the seasonal cycles of the mean values (calculated from seven lake stations) of inorganic and organic phosphate for both surface and bottom waters during 1954, 1955, and 1956. The mean vertical chlorinity range has been plotted on the same time scale, to indicate the periods of freshwater influence. Several interesting points arise from these plottings.

(i) Values remained comparatively uniform throughout 1954, except for a peak in the bottom inorganic figure. Inspection of the data shows that this was due to one isolated value in excess of 50 μg per litre at one station; the significance of the peak is therefore doubtful.

(ii) The rainfall discharge in the autumn period of 1955 introduced a large amount of organic phosphate into the surface waters; inorganic values remained at a low level.

(iii) During the same period a peak in the inorganic fraction was observed in the bottom waters. This could have been due to contributions either from the surface waters or from the bottom mud. In view of events in 1956 it is more likely to be the latter factor. There was no increase in the organic form equivalent to that in the surface waters.

(iv) In the surface waters the comparatively high organic fraction was maintained for the rest of the year, with insignificant variations in the inorganic fraction. However, in the bottom waters the inorganic values fell during the winter, and the organic fraction rose during the spring and fell to a minimum during the early summer.

(v) In 1956 maximum concentrations of inorganic phosphate were observed in the surface waters during the autumn discharge period. This phenomenon did not occur in the previous year, and therefore it is unlikely that it was caused by the rainfall discharge. The level of the organic fraction was much lower than in 1955.

(vi) As in 1955 there was considerable inorganic phosphate in the bottom waters. The possibility that vertical mixing transported some of this phosphate to the surface waters cannot be discarded, since the vertical chlorinity gradients were appreciably lower in 1956. The less violent discharge in this year could have resulted in a deeper homogeneous surface layer which transported phosphate from the bottom towards the surface, thereby producing the observed peak in 1956.

Intermediate values of chlorinity and temperature are not available for the discharge period of 1955, so that no comparison can be made between the depths of the surface layer in the two years; for this reason the explanation given above for the phosphate cycles may not be completely correct.

The whole question of wind stirring may be a vitally important one. In 1955, for example, the maximum values of organic phosphate which were associated with rainfall discharge fell to about 20 μg/l by the end of autumn, but were maintained at this level thereafter, without significant change in the inorganic fraction. It is quite possible that this effect was due to the vertical transfer of suspended material from the bottom to the surface, particularly as the organic fraction in the bottom waters fluctuated a good deal over the same period.

(b) *Nitrate*

The seasonal cycle of nitrate for surface and bottom waters is shown in Figure 15; mean values have once again been derived from seven lake stations. The autumn discharge periods of 1955 and 1956 were characterized by the increase of nitrate in the bottom waters, whereas in 1954 values remained low. The contribution of nitrate to the surface waters from Dora Creek and Cockle Creek was obviously low, so that production *in situ* is the only explanation for the observed high values in the bottom waters. The concentration of nitrate fell rapidly after the peaks had been reached, and no significant amounts were contributed to the surface waters.

Whereas the nitrate cycles can be compared with those of phosphate in the autumn periods of 1955 and 1956, there is no correlation between the two properties in October 1956. In this month surface values were very high in the channel and in the northern part of the lake. On the other hand the bottom values in the south and south-west region were also high; it is very difficult to explain these latter observations, but the high surface values could have been due to a large domestic effluent in the channel, and the subsequent circulation of this material into the northern lake.

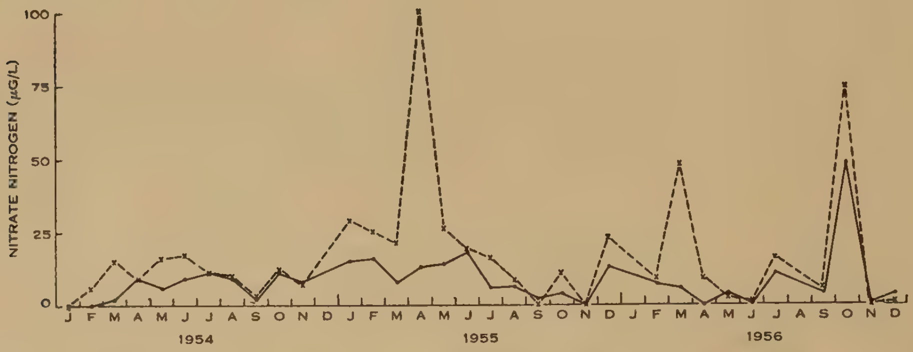

Fig. 15.—Seasonal cycles of nitrate in Lake Macquarie, 1954–56. The points shown represent the mean of seven lake stations, as in Figure 14. ————Surface; – – – – bottom.

(c) *Oxygen*

The association between the disappearance of oxygen and the development of a halocline is demonstrated clearly in Figure 16. Here the average chlorinity ranges in the vertical profiles of seven lake stations have been plotted on the same time scale as the average monthly oxygen saturation in the surface and bottom waters.

In 1954, a year of marine domination, the two lines remained constant; on the other hand the early autumn periods of both 1955 and 1956 produced appreciable haloclines, with which subsurface oxygen consumption was closely associated. No attempt was made to examine vertical oxygen profiles by sampling at intermediate depths; this fact leaves an unfortunate gap in our understanding of the nature and rate of oxygen removal.

The bathymetric features of Dora Creek are conducive to stratification, and in the deep regions deoxygenation is extreme. In the early stages of the investigations it was thought that the disposal of this stagnant water might affect the south-western region of the lake, but this is not so; the volume of water involved is not sufficient to produce a significant change in the characteristics of the lake water.

VIII. The Hydrological Regime

The lake is a marine-dominated body of water in which the nutrient levels are low and similar to those of the adjacent sea but greater than those in the freshwater drainage into the lake other than organic phosphate which is high during periods of flood.

The extended periods of high chlorinity (Section V) indicate little freshwater discharge for most of the year. There is relatively little tidal ventilation owing to the shallow and narrow entrance which also restricts the outward passage of flood waters. As a consequence, despite the relatively small volume of freshwater entering the lake even during periods of heavy rain its dispersal to sea is slow and conditions of stratification can occur, resulting in a lowering of the oxygen levels in the underlying salt water.

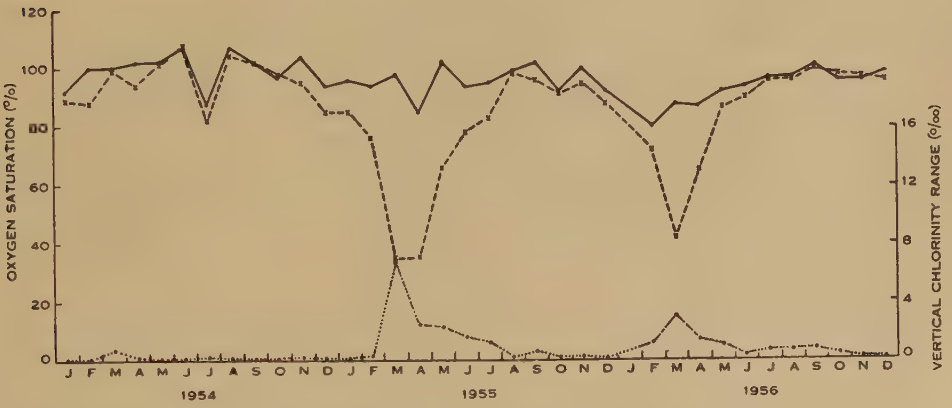

Fig. 16.—Relationship between the distribution of dissolved oxygen and the vertical chlorinity range, 1954–56. The points shown are derived as in Figures 14 and 15. ———— Surface oxygen saturation; – – – – bottom oxygen saturation; ······· chlorinity.

Except during flood periods the lake water is homogeneous in most properties both vertically and horizontally. Truly marine water is detectable only in the vicinity of the entrance during flood tide. It rapidly loses its identity as it disperses into the lake.

There is a wind-induced circulation in the lake which is shown separately in the northern and southern parts, as the shallows between Swansea and Wangi effectively bar deep water movement.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

III. CHARACTERISTICS OF WATER AND MUD

By L. G. M. Baas Becking*

[*Manuscript received February* 5, 1959]

Summary

The water of Lake Macquarie is very similar to sea-water though deficient in total base.

The deep muds are of a fine silt, partly oxidized, with an E_h about +225 mV. Reduced muds (−75 mV) have been found only in semi-isolated places such as "The Hole". The mud contains only a small clay fraction and includes very little iron compared with most estuarine muds. This lack makes the bottom muds theoretically susceptible to calamitous sulphate reduction when the oxygen level of the superjacent water is lowered, as happens when stratification follows rainy periods.

I. WATER

The waters of Lake Macquarie, apart from a lowering of the chlorinity which is particularly noticeable in the surface waters (Spencer 1959), are characterized by average base values (Fig. 1) at a rather high chlorinity (Table 1). In this respect, Lake Macquarie is like the water of the Georges River and Port Hacking River and different from other estuarine waters which have been studied (Fig. 2).† The average depletion in base observed in Lake Macquarie is about 25 per cent. Similar values have been observed in Georges River. It is suggested that the preponderance of the fine bottom silt accounts in part for the low base values or, since most changes in total base are biological in origin (Baas Becking 1956*b*), that a bottom animal (such as *Maldane*) is the cause.

The total base is also influenced by dilution, varying from 1×10^{-4}N in Dora Creek to $2\cdot 3\times 10^{-4}$N near the entrance, and because it is a function of pH, it has a tendency to diminish in the more acid environments. The pH of the water, in contrast with that of the mud, is steady (Fig. 3). Over *Enteromorpha*, in the shore zone, it may reach a value of 9·0 in the afternoon and in the deeper waters it may decrease to 7·2. In this respect the waters of Lake Macquarie are very much like other estuaries. The electrode potential of the water is high (Figs. 3 and 4), well above +110 mV, which is the maximum E_h at which sulphate reduction can occur; however, no samples were taken from deep water under the occasional conditions of stratification.

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†Lake Illawarra, George's Basin, Lake Conjola, Coila, Tuross, and Merimbula (New South Wales); Mallacoota and the Gippsland Lakes (Victoria).

The values for total phosphate and nitrate are not significantly different from those of sea-water (Spencer 1959). Complete exhaustion of phosphate in the water, as frequently occurs in offshore waters, was never observed in the lake. Summarizing, the average water of Lake Macquarie differs but little from sea-water and no depletion in phosphates has been observed in three years of investigation.

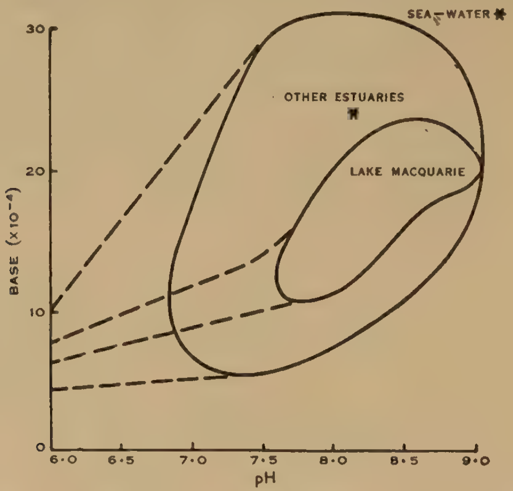

Fig. 1.—Total base as a function of pH in Lake Macquarie as compared with other estuaries.

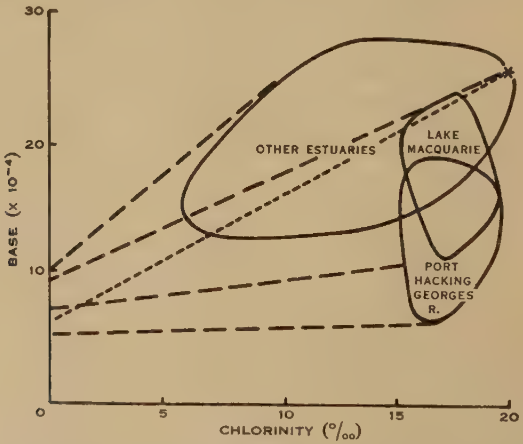

Fig. 2.—Total base as a function of chlorinity in Lake Macquarie, Georges River, Port Hacking, and other estuaries.

II. Bottom Material

The shore material, populated by submerged phanerogams and algae, is sandy near the entrance with varying admixtures of mud and rock elsewhere. The slope, inhabited chiefly by mussels, contains the maximum of shell debris, while the deeper parts are covered by fine, silty, greyish to blackish brown muds, mostly in a fairly oxidized condition. In the frequency diagram (Fig. 4) the peak at E_h +325 mV corresponds to the aqueous phase, the lesser peak at +225 mV represents the partly oxidized mud. Reduced muds (peak at −75 mV) are found chiefly in the southern part (The Hole). The lowest potentials occurred near the outflow of a food factory on Dora Creek (Spencer 1959, Fig. 1, Station 2). Here the lowest pH value, 5·1 (Fig. 3), also occurred. However, this increase in acidity was not accompanied by phosphate release, as observed in other deeper muds elsewhere (Baas Becking and Mackay 1956). This may be due to the nature of the organic matter in the effluent.

TABLE 1

PROPERTIES OF MUD AND WATER, LAKE MACQUARIE

Characteristic	Lake Macquarie			Other Estuaries		
	Low	Mean	High	Low	Mean	High
Water						
Cl (‰)	0	18·5	20·0	0		20·0
P (μg/l)	22·2	28·3	33·2			
N (μg/l)	12·3	20·2	50·5			
pH	7·2	7·9	9·0	6·8	8·0	9·1
E (mV)	+190	+320	+460			
Excess base ($\times 10^4$N)	1·0	1·85	2·3	0·6	2·10	2·7
Mud						
Specific gravity	2·14	2·33	2·50	2·03	2·50	2·90
Iron (%)	0·33	0·62	0·96	0·31	3·32	14·0
Organic matter (%)	4·0	13·0	21·0	0	14·0	26·0
$CaCO_3$ (%)	28·0	34·0	47·0	3·0	23·0	47·0
Phosphate (P%)	0·100	0·125	0·150			
pH	5·10	7·42	9·42	5·3	7·6	9·4
E (mV)	−220	+154	+590	−380	+200	+500

The "*Maldane* mud" of Lake Macquarie contains very few particles larger than 400 μ, and about 70 per cent. of all particles are smaller than 100 μ. Apparently these represent an undisturbed process of deposition of very fine particles and give evidence of the absence of bottom currents.

Microscopic examination of the mud from Lake Macquarie shows a large amount of fine calcium carbonate, organic matter, quartz, sponge spicules, and diatom frustules. There is some pyrite, but no magnetite. The clay minerals are few and confined to the 0–100 μ fraction where they amount to a quarter of the total. In its low content of clay mineral the mud reflects the podzolic nature of the sediment–soil complex carried by the runoff.

The separation of the fractions by settling in liquids of different gravity was performed on seven samples of mud, one from the shore, one from the slope, and five from the bottom muds (Table 2).

The shore mud shows a bimodal frequency distribution of densities; there is still, incorporated in the component particles, a large amount of organic matter not "assimilated". Similar muds were encountered in several estuaries such as Lake Conjola, Lake Coila, Lake Mallacoota, Shell Point (Georges River), and Port Hacking River.

In the slope mud there is a decrease in the fractions of *c.* 2·5 specific gravity and an increase of the fractions of *c.* 2·0 specific gravity. This is due to an increase in the amorphous silica content (diatoms), sponge spicules, and a decrease in quartz content. Although there is more heavy fraction in the slope mud than in the shore material, the average specific gravity is much lower, owing to the disappearance of the sand.

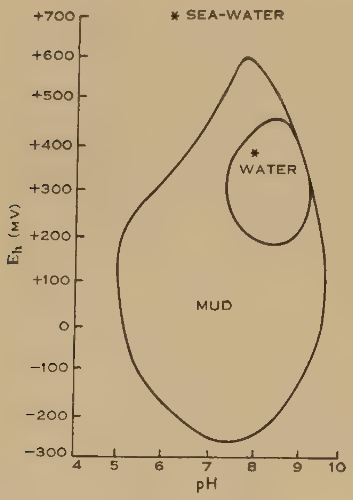

Fig. 3.

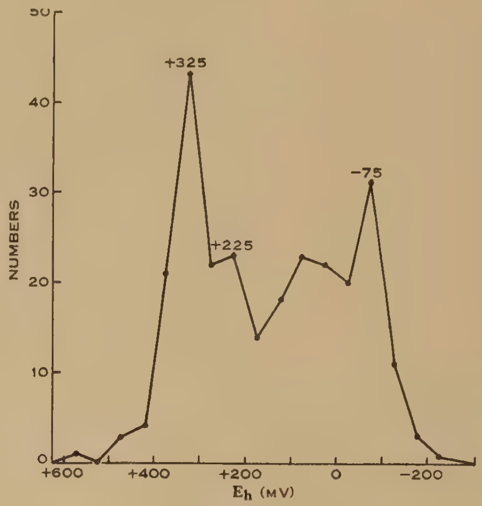

Fig. 4.

Fig. 3.—E_h as a function of pH of water and mud in Lake Macquarie.
Fig. 4.—Frequency diagram of E_h in Lake Macquarie muds.

The bottom mud shows a decrease in specific gravity from the fine to the coarser particles. The coarser fractions, 200–300 μ and 300–400 μ respectively, are very much alike both in average specific gravity and in the nature of the frequency distribution (Fig. 5). From Table 1 it appears that the average mud from Lake Macquarie has a slightly lower specific gravity than the average estuarine mud, owing to the low clay content.

While the total organic matter (determined by loss on ashing with deduction of 6 per cent. of the amount of clay mineral) seems normal (Table 1), the ratio of iron to organic carbon is abnormally low. X-ray analysis of the *Maldane* mud shows that apart from haematite and calcite, small amounts of dolomite and kaolinite could be detected. The dolomite is usually derived from calcite in a sea-water environment, while the kaolinite is an end product of laterization.

Figure 5 shows the relation between organic matter and Fe (expressed as lepidocrocite, O : Fe·OH) in various estuaries, in a deep sea deposit, and in a coral reef. The ratio of iron oxide to organic matter (calculated as $C_6H_{10}O_5$) is, in Lake Macquarie, more than 9 : 1, while the average of all estuarine and reef situations is about 2 : 1. Inasmuch as the iron seems to enter in a loose combination with organic matter, Lake Macquarie mud may contain much free organic substance.

TABLE 2

SEPARATION OF FRACTIONS BY SETTLING IN LIQUIDS OF DIFFERENT SPECIFIC GRAVITY

Sp. Gr.	Percentage of Fraction						
	*Z**	*T*	*M*	0–100 μ	100–200 μ	200–300 μ	300–400 μ
3·4	1						
3·3	2	1					
3·2	2	1		1	1		
3·1	4	0		1	2	1	1
3·0	3	1		3	2	1	1
2·9	6	1		5	2	1	1
2·8	6	2		10	4	1	1
2·7	9	2	1	13	5	2	2
2·6	12	2	10	12	8	4	3
2·5	14	3	23	14	12	8	6
2·4	10	4	15	11	19	13	11
2·3	6	6	13	10	18	18	18
2·2	5	15	10	8	14	20	20
2·1	3	18	9	5	8	16	17
2·0	11	18	8	3	4	10	15
1·9	5	11	6	2	2	5	4
1·8	6	8	3	1			
1·7	5	5	2	1			
1·6		2					
Mean	2·43	2·14	2·30	2·50	2·41	2·27	2·26

General mean 2·33 ± 0·17

**Z* = shore, *Zostera* predominating; *T* = slope, *Trichomya* predominating; *M* = mud, *Maldane* predominating.

The lime content of the mud is high and fairly constant as compared with the average for all estuarine environments. Phosphate content is about twice as high as the average, and much less variable than the values for other estuarine muds (Table 1).

III. THE OCCURRENCE OF FETID BLACK MUD

After heavy rains stratification develops and the saline bottom layer becomes isolated (Spencer 1959). This isolated bottom layer may subsequently spread owing to the action of wind. It shows a marked depletion in oxygen; during this survey

(1953–57) the average oxygen saturation in the bottom water dropped to *c.* 30 per cent., although lower values were observed. It was pointed out earlier that the iron content of the mud is low in comparison with that of other estuaries. This means that, if the isolation of the bottom water should continue over a longer period, sulphate reduction would start to preponderate over oxidative processes, and H_2S and SH^- would be generated. The ferrous and ferric oxides and hydroxides would act as a sulphide trap, probably forming the hydrotroilite Fe(OH)(SH). The iron is present in small quantities and would rapidly be saturated by sulphide to form $Fe(SH)_2$ (Baas Becking 1956*a*). This compound occurs often as a stable, ink-black suspension, completely deoxygenating the environment.

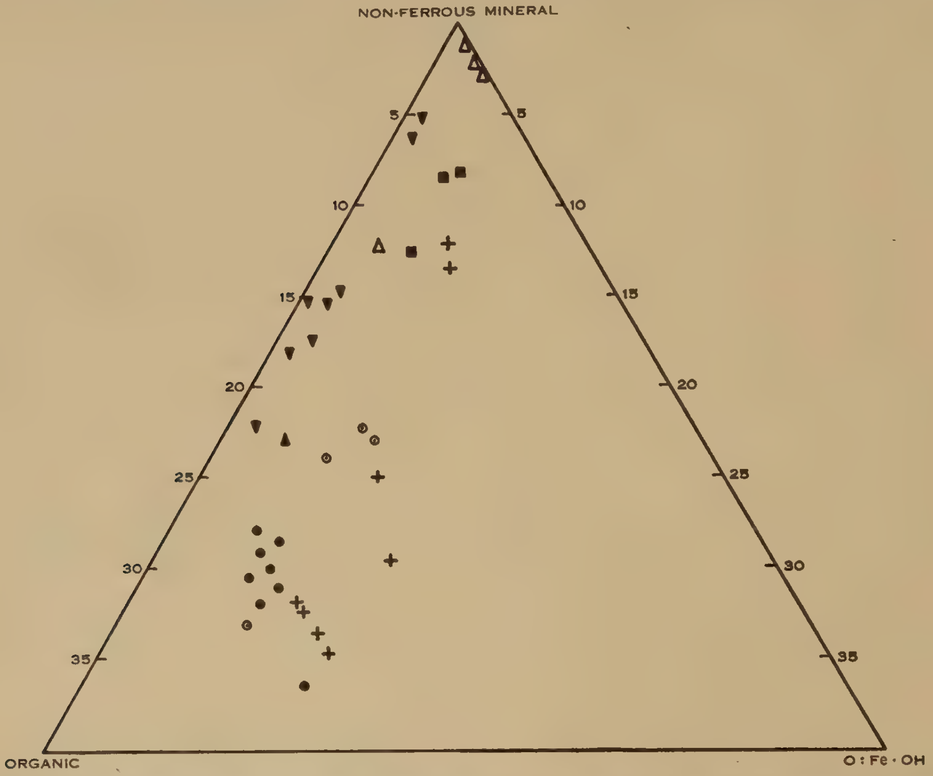

Fig. 5.—Correlation diagram between organic matter, iron, and non-ferrous minerals in various estuaries and in a coral reef.

▼, Lake Macquarie, N.S.W.
⊙, Silt traps, Shell Point N.S.W.
△, Fish pond, Port Hacking, N.S.W.
●, South-west arm, Port Hacking, N.S.W.
▲, Crawley Bay, Swan River, W.A.
■, Pittwater, Tas.
+, Coral reef, Noumea, New Caledonia.

IV. Acknowledgment

Mr. D. Haldane, of the Bureau of Mineral Resources, Canberra, kindly carried out the X-ray analyses referred to in Section II.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

IV. BACTERIAL AND FUNGAL STUDIES

By E. J. F. Wood*

[*Manuscript received February* 5, 1959]

Summary

Bacterial communities in Lake Macquarie show several peculiarities including the paucity of cellulose digesters and agar digesters, and the presence at times of anaerobic sulphur bacteria in waters containing considerable oxygen.

The E_h of the lake bottom is frequently positive, negative potentials being recorded from decomposing *Zostera* patches and from the microbially rather inert blue muds. The latter show little or no active sulphate reduction, though *Desulphovibrio* may be present. Photosynthesis controls the pH on the sea-grass flats, values as high as 9·7 having been recorded off Swansea flat on a sunny afternoon.

Bacterial populations are relatively low, especially in the muds, and there is no marked seasonal variation.

Contamination by faecal pollution of the lake waters could not be demonstrated, either during the summer holiday season or during a typhoid epidemic at Swansea.

I. MICROBIAL ENVIRONMENTS

The shallow areas of Lake Macquarie consist largely of gravels round the northern and north-western shores from Croudace Bay to Wangi, and of sands and sandy muds from Myuna Bay to Belmont. Both gravels and sands were found to have a positive E_h except where *Zostera* was decomposing (Table 1(*a*)); the negative E_h values were due to sulphate reduction, and *Desulphovibrio* was isolated from the bottoms in each case (for methods see Baas Becking and Wood 1955).

Table 1(*b*) gives pH/E_h values for bottoms in one transect across and one along the lake and again shows a relation between the nature of the bottom and the redox potential, gravel and sandy bottoms having positive E_h values, except when decaying *Zostera* was present, and the muds negative values. The pH/E_h values for mud profiles of Lake Macquarie are given in Table 2. The variations at The Hole and at Swansea are noteworthy, and result from the stage reached by the *Zostera* community. When the plants are growing actively (Swansea 3 and 4), the E_h is positive and relatively high; when they are quiescent or decaying the E_h falls, and *Desulphovibrio* can usually be isolated. There was rarely an odour of hydrogen sulphide in the muds, and *Desulphovibrio* was often absent. For example, this organism was isolated only at Stations (*b*)(i)6 and (*b*)(ii)1, 11, 12, 13, and 14, at the time the E_h values were recorded (Table 1). The high pH at (*b*)(ii)10 was due to the photosynthesis of *Zostera* and *Ruppia* on the Swansea flat, the sample being taken at 2.45 p.m. on a sunny day. The pH values (Table 1(*a*)) are lower farther from shore.

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*Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, N.S.W.

TABLE 1

pH AND E_h MEASUREMENTS OF BOTTOM MUDS IN LAKE MACQUARIE

(Readings were taken at the surface of the mud)

Station	pH	E_h (mV)	Bottom
(*a*) *Shore-Line Survey* (taken in 4–18 in. of water)			
Belmont Jetty	7·34	−90	decaying *Zostera*
Speer's Point	7·62	+60	gravel
Croudace Bay	7·20	−50	decaying *Zostera*
South Creek	7·10	+130	growing *Zostera*
Warner's Bay	7·65	+100	growing *Zostera*
Marmong Point (surface)	7·35	+180	gravel
Marmong Point (15 cm)	8·3	+190	gravel
Marmong Point (inshore)	8·1	+40	gravel
Bolton Point	8·1	+70	gravel
Toronto Jetty	8·1	+30	gravel and sand
Swansea flat	7·1	+60	growing *Zostera*
Belmont flats	6·1	+185	growing *Zostera* and *Posidonia*
Cockle Creek (mouth)	6·85	+45	growing *Zostera* on gravel
Kilaben Bay	7·9	+220	gravel
Myuna Bay	7·62	+52	growing *Zostera*
Myuna Bay	7·93	+180	growing *Zostera*
Fennell Bay	6·30	+150	growing *Zostera*
Dora Creek	6·85	+155	growing *Zostera*
Lake Erraring	7·25	+105	growing *Zostera* and *Ruppia*
The Hole	6·70	+90	growing *Zostera* and *Ruppia*
(*b*) *Transects*			
(i) Mark's Point to Fishing Point (Stations at 10-min intervals)			
1	7·7	+250	sand
2	7·7	+250	sand
3	7·1	+50	mud
4	7·4	−60	mud
5	7·5	−40	mud
6	8·0	−120	mud
7	8·0	−85	mud
(ii) Crangan Bay to Speer's Point (stations at 15-min intervals)			
1 Crangan Bay shore	5·9	−130	decaying *Zostera*
2 Crangan Bay	7·5	+100	sand and mud
3 opposite Nord's Wharf	8·0	+100	sand and mud
4 opposite Cam's Wharf	7·5	−50	mud
5 Point Morisset	7·5	−50	mud
6 off Pulbah	7·9	−75	grey mud
7 S. of Wangi Point	7·5	−50	grey mud
8 Wangi Point	8·2	0	black sand and mud
9 off Swansea	7·2	−100	mud
10 edge Swansea flat	9·2	+150	*Zostera* on sand
11 NW. of Swansea	7·9	−180	mud
12 off Mark's Point	8·3	−180	mud
13 off Coal Point	8·0	−100	mud
14 off Gravel Point	8·0	−170	mud
15 off Green Point	7·5	−90	mud

This may be due to greater photosynthetic activity nearer the shore, especially near the flats. The zero E_h value at Wangi was obtained where the bottom consisted of black organic mud, and no sulphate-reducers were ever isolated from this station.

There are no deficiencies of the common nutrients, e.g. phosphorus and nitrogen (Spencer 1959), and this is borne out by the relatively uniform growth of heterotrophic bacteria throughout the year as shown in Figure 1.

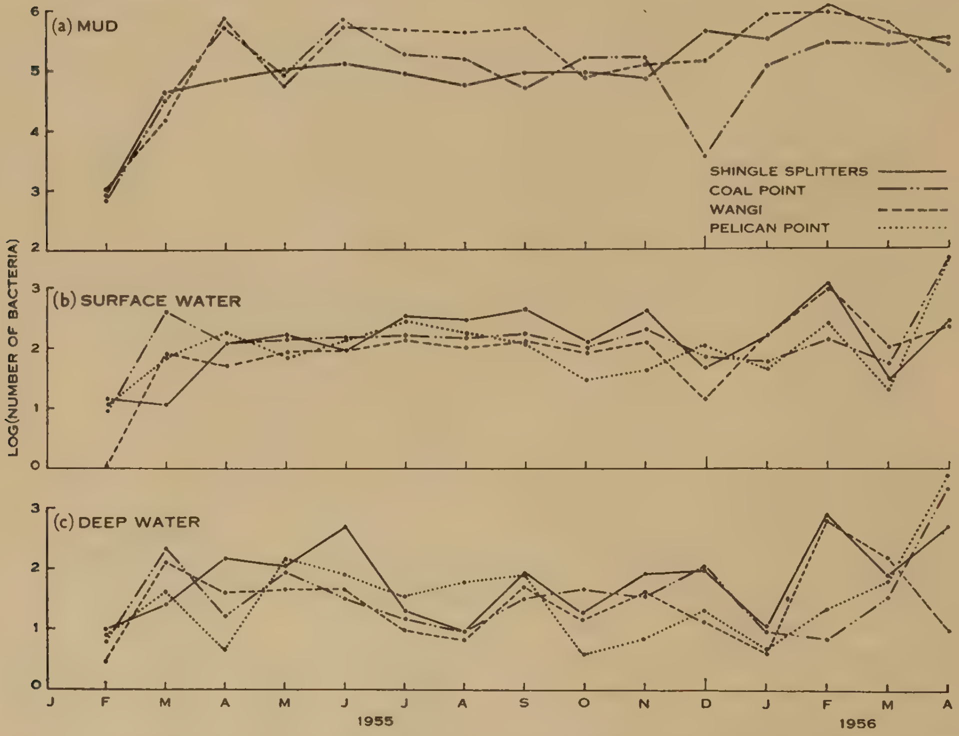

Fig. 1.—Logarithms of the number of bacteria occurring in (*a*) mud, (*b*) surface water, and (*c*) deep water.

II. Bacteria

The bacteriology may conveniently be divided under the following headings: autotrophic bacteria, heterotrophic bacteria, and contamination (by coliform bacteria of faecal origin).

(*a*) *Autotrophic Bacteria*

(i) *The Sulphur Cycle.*—Baas Becking and Wood (1955) have shown that the sulphur cycle can be taken as a measure of the microbial activity of an estuary. The major seat of activity, as demonstrated by the emission of hydrogen sulphide, is in the muds of the *Zostera* and *Ruppia* flats. However, in some cases, sulphur bacteria were found in the blue muds and in the water of the lake. Hydrogen sulphide could rarely be demonstrated in the blue silty muds, which were oxidized and stable, showing that the colour was largely due to organic matter rather than to ferrous sulphur compounds. The redox potential of the blue muds and of the mussel zone lay generally within the potential sulphate-reducing range, i.e. below +100 mV (see Table 1).

Within the sea-grass association, the redox potential of the surface muds was usually positive, especially in the gravels of Permian origin, from Wangi north and east to Mark's Point. In the late summer to autumn, when there was a heap of rotting *Zostera* along the shore-line, local drops in E_h occurred. The *Ruppia–Zostera* muds in The Hole, the *Enteromorpha–Zostera* flats in Whitehead's Lagoon, the *Zostera* flat outside this lagoon in Myuna Bay, and a small area near the outfall of drains from the National Fitness Camp at Cape Wolstoncroft were the only areas where hydrogen sulphide was produced almost continuously and to any extent. In the summer (February–March), when the winds moved masses of the rotting *Zostera* through the lake, *Desulphovibrio* and *Thiobacillus denitrificans* could be isolated from both surface and deep water, though they might not be found in the mud below. This phenomenon was observed at Shingle Splitter's Point and Coal Point and off Pelican Island, but not off Wangi. Oxygen depletion was not evident at this time. From this it seems that the sulphur bacteria, though present in the water, were not actively causing reduction of sulphate.

When sulphate reduction occurred, there was usually an oxidation zone containing *Thiobacillus thioparus* in the first 5–15 cm, below which the redox potential was negative (see Table 2, Lake Erraring, The Hole 1). If there was a heavy growth of *Enteromorpha*, *Vaucheria*, or a considerable amount of decaying *Zostera* in contact with the mud surface, the redox potential was sufficiently reduced to allow sulphate reduction right to the surface (Table 2, Whitehead's Lagoon, The Hole 4). If this occurs, there is a likelihood of purple bacteria occurring in the metabiosis, or, if the organic matter is sufficiently high and the hydrogen sulphide gradient right, *Beggiatoa*, *Thiothrix*, or *Thiovulum* occur. These organisms form films or veils where hydrogen sulphide is available on one side and oxygen on the other. At times, when sulphate reduction was localized in pockets of rotting *Zostera*, or algae, there was an oxidation zone below the reducing zone (Table 2, Swansea 1). If the deposition of decaying organic matter was relatively continuous, as in the Whitehead's Lagoon and Wyee 4 profiles, there was no oxidizing zone below the reducing zone. In these muds, there was usually a minimum pH at 15–20 cm depth, as is shown in the majority of these profiles.

On the Swansea flats, the redox potential was negative through the spring and summer months (Swansea 1 and 2), while there was active growth and decomposition of *Zostera* and the algae. In the winter, however, when the flats were bare, the redox potential became positive (Swansea 3 and 4). In the shallow, almost enclosed Hole, which is fed by a swamp and has a tendency to stagnation, the E_h was relatively low throughout the year, and iron bacteria (*Sphaerotilus*) occurred on the mud surface at, or just above, the water-line.

A general picture of the pH and E_h of the bottom shows a maximum at the surface and at 30 cm and the E_h has also the greatest spread at these levels. The pH of the water did not fall below 7 at any time, and the E_h did not fall below +100 mV, thus sulphate reduction in the water was never possible.

TABLE 2

REDOX POTENTIALS AND pH VALUES OF MUD PROFILES

(E_h in mV)

Depth of Profile (cm)		0		5		10		15		20		25		30	
Stations		pH	E_h	pH	E_h	pH	E_h	pH	E_h	pH	E_h	pH	E_h	pH	E_h
Whitehead's Lagoon		9·20	−100			9·30	−20							9·30	−33
Lake Erraring		8·31	+200			8·22	−170							8·08	−15
The Hole (Wyee)	1	7·45	+160			8·10									
	2	7·71	+55	7·42	+50	6·90	−25	6·85	−63	6·50	−55	7·12	−75		
	3	7·81	+65	7·12	−10	6·50	−55	6·11	+40	6·80	−55				
	4	7·72	+30	7·60	−65	8·40	−55	8·30	−120	7·80	−120				
Swansea	1	7·41	+85	6·35	−35	6·15	−17	6·10	−50	6·65	−72	6·42	−80	6·80	+250
	2	5·51	+50	6·35	−75	6·12	−120	6·70	−75	7·02	−100	6·82	−10		
	3	7·85	+215	7·52	+225	7·58	+240	7·80	+220	7·35	+230	7·51	+100	8·00	+280
	4	7·61	+200	7·32	+240	7·54	+195	7·60	+180	7·53	+185	7·60	+193		
Mean pH		7·8		7·1		7·5		7·1		7·3		7·1		8·1	
Mean E_h		+96		+56		−2		−40		−8		+30		+111	

(1) Desulphovibrio.—In Lake Macquarie *Desulphovibrio desulphuricans* has been isolated (by the method described by Baas Becking and Wood 1955) in the Hole, Myuna Bay, Cape Wolstoncroft, Whitehead's Lagoon at all times, and from Swansea flats, and the offshore stations off Pelican Island, Shingle Splitter's Point, and Coal Point in the late summer.

(2) *Thiobacilli.*—The anaerobic sulphur-oxidizing organism *Thiobacillus denitrificans* was isolated by the method of Waksman (1933) from 43 per cent. of the test cultures from the sea-grass community at The Hole, Whitehead's Lagoon, and Myuna Bay (i.e. the principal areas of sulphate reduction where the cores were anaerobic), from deep water and mud, and on one occasion, from surface water off Shingle Splitter's Point and Coal Point in the late summer.

Thiobacillus thioparus, a sulphur-oxidizing organism which reduced the pH of the medium from 7·5 to 4·5 aerobically, was isolated from The Hole, Shingle Splitter's Point, Dora Creek (mouth), Lake Erraring, Myuna Bay, Cockle Creek, and Belmont by the method used by Baas Becking and Wood (1955). It was identical with the organism previously described from other estuarine localities by Baas Becking and Wood (1955).

(3) Beggiatoa, Thiothrix, Thiovulum.—*Beggiatoa mirabilis* was found on the surface of the mud and dead *Zostera* close to the effluent of the National Fitness Camp at Cape Wolstoncroft, where there was strong sulphate reduction and the organic content of the mud was high. *Thiothrix* was mixed in with *Beggiatoa* at times.

The peculiar, film-forming motile organism *Thiovulum* was also observed on rotting *Zostera* near this effluent and down-wind from it. Field observations suggest that these organisms may require organic matter, possibly organic sulphides. Scotten (1953) grew *Beggiatoa* spp. on organic media without sulphur.

(4) *Purple and Green Bacteria.*—A *Chromatium* was isolated on Wassink's medium from Whitehead's Lagoon, where this organism habitually grows on rafts of decomposing *Zostera* and *Enteromorpha* in the shallows. In the spring, patches a square yard or more may be coloured pink by this *Chromatium*. It is interesting to record that when purple bacteria are present in such situations small fish are abundant. Green sulphur bacteria (*Chlorobium*) were isolated from muds and from decaying *Trichomya* taken from 20 ft below high water mark in the lake, and purple sulphur bacteria later appeared in the samples.

(ii) *Iron Bacteria.*—*Sphaerotilus* was found at The Hole and at the mouth of Dora Creek. In each case, the iron bacteria were in a gradient zone, above sulphate reduction (Baas Becking, Wood, and Kaplan 1956).

(*b*) *Heterotrophic Bacteria*

(i) *Nitrogen Fixation.*—Bacteria of the sulphur cycle—*Desulphovibrio* (Sisler and ZoBell 1951) and the purple and green sulphur bacteria (Lindstrom, Burris, and Wilson 1949)—and blue-green algae belonging to the Nostocaceae, which have been demonstrated in Lake Macquarie, are capable of fixing dissolved nitrogen. *Azotobacter*, however, could not be isolated either in Wang's synthetic medium with benzoate or on a slightly modified basal medium (Y. T. Tchan, personal communication) using ethanol as a carbon source.

(ii) *Chitin Digestion.*—This was found to be very active in all parts of Lake Macquarie in both mud and water, especially in May and again from September to December, up to 100 chitin digesters being present in a gram of mud, and from 10 to 100 per ml of water. In these months, all cultures made were positive, and there was some activity throughout the year. Tests were made according to the method of Hock (1940).

TABLE 3

PROTEOLYTIC ACTIVITY OF BACTERIA FROM DIFFERENT ENVIRONMENTS

The values show the percentage of samples giving a particular reaction

Reaction	Environment		
	Surface Water	Bottom Water	Mud
Litmus milk			
Peptonized	23	73	84
Coagulated	0	9	0
Alkaline	47	18	0
Decolorized	30	0	0
Gelatin			
Liquefied	40	70	100
Softened	20	8	0
Unchanged	40	22	0
Fish protein			
Digested	0	0	0

(iii) *Cellulose Digestion.*—Cellulose-digesting bacteria were sought by using media containing cellulose with and without organic nitrogen sources. No digestion could be demonstrated in aerobic or anaerobic cultures on sea-water media. This is surprising in the light of the quantity of cellulose-containing plants occurring in Lake Macquarie and in Australian estuaries. However, there are deep beds of the cellulosic parts of *Zostera* above the water level round the lake, giving field support to the laboratory findings regarding the absence of cellulose digesters. It is difficult, however, to believe that cellulose-digesting bacteria or fungi were entirely absent.

(iv) *Agar Digestion.*—Agar-digesting bacteria were infrequent on both nutrient and non-nutrient agar media. Even cultures made directly from red algae gave little active digestion on non-nutrient agar. The organisms that were isolated digested agar very slowly, merely forming a depression and in no case completely dissolving the agar as does *Pseudomonas gelatica* (Gran) Bergey *et al.*

(v) *Lignin Digestion.*—Of cultures set up for lignin digestion, i.e. with lignin as the sole nutrient source, about 8 per cent. were positive in winter and 60 per cent. in late summer (March). The positive cultures were obtained from muds and from surface and deep water samples from Shingle Splitter's Point, Wangi, Coal Point, and Pelican Island. Lignin digesters included bacteria (chiefly Actinomycetes), and fungi.

(vi) *Proteolysis* (see Table 3).—Proteolysis was tested for by litmus milk, gelatin, and fish protein, using the media described by Wood (1940). The absence of bacteria capable of lysing fish protein is noteworthy, and is in conformity with the specificity of bacterial floras of marine communities suggested by Wood (1953).

TABLE 4

OCCURRENCE OF BACTERIA IN VARIOUS ENVIRONMENTS

Species	Water			Sea-Grass Community (%)
	Bottom (%)	1 m from Bottom (%)	Surface (%)	
Bacillus subtilis	45·0	39·5	22·0	10–25·0
B. megatherium	18·0	7·0	5·5	0
B. sphaericus	0	7·5	0	0
Corynebacterium globiforme	0	7·0	0	5·0
C. flavum	0	0	0	10·0
C. miltinum	0	0	0	5·0
Actinomyces sp.	18·0	0	5·5	10–25·0
Staphylococcus candidus	0	8·0	8·0	0
S. roseus	0	8·0	0	0
Mycoplana dimorpha	19·0	23·0	54·0	40·0
M. citrea	0	0	0	5·0
Sarcina lutea	0	0	5·5	0
Pigmented strains	20	38	27·5	50
Ratio of gram-positive to gram-negative forms	1·9	2·0	0·7	0·9

Note: The ratios of different bacterial species were relatively constant throughout the year except in the sea-grass community where the numbers of spore-formers and Actinomycetes varied considerably.

The ability of the bacteria to attack milk and gelatin increased from surface water to mud, as is shown in Table 3. None of the strains examined contained a urease when tested by the method of Wood (1950).

(vii) *Taxonomy.*—Determinative studies were made on the bacterial flora isolated from Lake Macquarie, using the same criteria as those of Wood (1953). Water samples were taken with a J-Z water sampler (ZoBell 1946), and mud samples with a small grab, only the centre portion of the sample being used. Samples from the sea-grass community were taken from a number of localities around the lake. Results are recorded in Table 4.

The bacterial flora of Lake Macquarie differs from the estuarine floras recorded by Wood (1953) which were mainly derived from Botany Bay, Port Hacking, and Port Jackson, in having a greater number of spore-formers and Actinomycetes, with fewer gram-negative elements. The ratio of gram-positive to gram-negative elements decreases from bottom to surface. The differences observed are in accord with the lower salinity of Lake Macquarie, since the bacterial flora has more in common with the soil floras (Fig. 2).

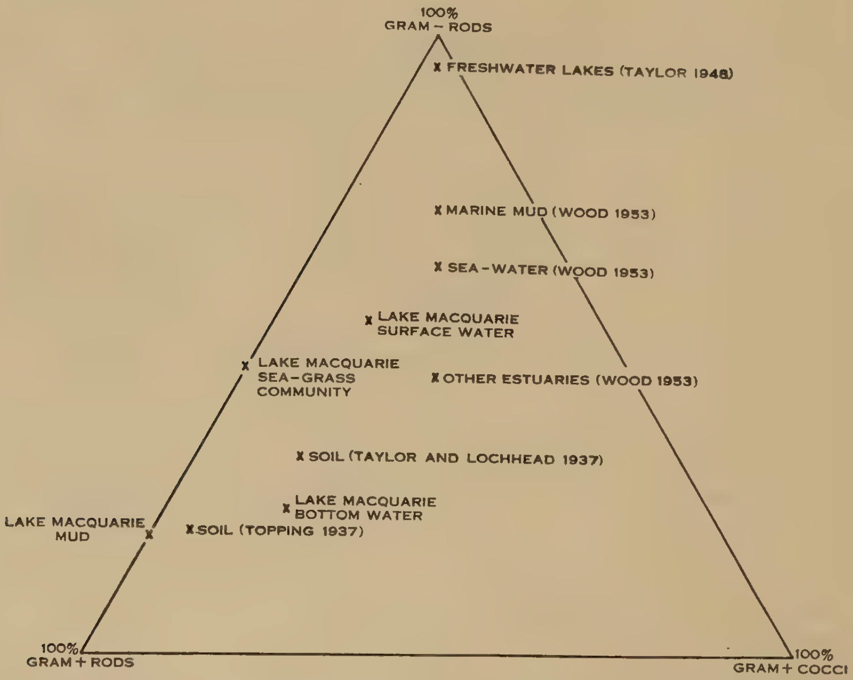

Fig. 2.—Comparison of the bacterial floras of various environments, indicating that that of Lake Macquarie has more in common with soil floras than with truly marine floras.

(viii) *Bacterial Population Studies.*—Bacterial counts were made from five offshore stations: off Shingle Splitter's Point, Wangi, Myuna Bay, Coal Point, and Pelican Island. Plate counts made on nutrient agar from the mud bottom showed relatively low figures for viable heterotrophs (Fig. 1(*a*)). It will be seen from the graph that the bacterial count reached 10^6 organisms per gram on one occasion, in February 1956 during very heavy and continued rains. At this time, there was increased activity of both heterotrophs and autotrophs. The mud counts do not show any marked seasonal variation, that from Shingle Splitter's Point showing less than the two others. There was a sharp rise from February to March 1955, associated with summer rains, and a sharp drop at Coal Point in December. These counts are, in general, much lower than those made by Potter and Baker (1956) in a freshwater lake of comparable size.

Viable counts from the water at the surface and 1 m from the bottom at the same stations and at Pelican Island are shown in Figures 1(*b*) and 1(*c*) respectively. They varied almost at random from February to June 1955 but the bottom counts were lower than the surface counts from July to November and again in January and February 1956. In March–April 1955 and again in those months in 1956, the bottom count was higher than the surface count at Coal Point and Shingle Splitter's Point but not at Wangi, where the lake is strongly constricted, and where there are other peculiarities (see above). The sudden rise in the counts at Pelican Island and Coal Point in April 1956 suggests an inflow of water from the entrance striking across the lake at that time. The bacterial population of the water is comparable with that of Potter and Baker (1956) for Flathead and Rogers Lakes, Montana.

TABLE 5

NUMBER OF HETEROTROPHIC BACTERIA CLOSE TO SHORE

Location	Water Bacteria (per ml)	Mud Bacteria (per g)
Toronto	2840	$5 \cdot 8 \times 10^5$
Cockle Creek (mouth)	129	$2 \cdot 4 \times 10^6$
Warner's Bay	2336	$4 \cdot 5 \times 10^6$
Fennell Bay	10496	$2 \cdot 0 \times 10^6$
Swansea flat	1920	$3 \cdot 4 \times 10^6$
The Hole	50	$6 \cdot 5 \times 10^6$
Belmont flat	250	$6 \cdot 8 \times 10^5$
National Fitness Camp		
(east)	200	$1 \cdot 3 \times 10^6$
(west)	200	$2 \cdot 8 \times 10^5$

It seems that, during 1955, there was a correlation between the bacterial counts and the counts of net dinoflagellates with the latter a month behind in phase until September, and from December 1955 to April 1956 the counts are in phase (Fig. 1). The diatom counts, on the other hand, have a general negative correlation with the bacterial counts.

Plate counts which were also made at onshore stations from the water above the *Zostera* and *Ruppia* beds varied considerably as the figures in Table 5 show.

The high count at Fennell Bay was probably associated with the enrichment from the sewage treatment plant on Stoney Creek. The bottom counts were higher, on the whole, than those of the blue mud except in the coarse gravels at Toronto, Belmont, and on the west side of the National Fitness Camp at Cape Wolstoncroft.

(*c*) *Contamination*

Throughout the summer of 1953, i.e. during the holiday period, when the population was increased by a number of visitors, the waters were examined for coliform organisms at the following stations: Dora Creek (mouth and railway bridge), Avondale dam, Dora Creek near Stockton Creek, and Cockle Creek (mouth, road bridge, sanitary depot). Water samples of 10 ml and 1 ml were inoculated into tubes of lactose–bile broth, incubated at 37°C for 24–48 hours, and all tubes giving gas were inoculated into brilliant green–bile broth and peptone water, incubated at 45°C for 24 hours, and checked for gas and indole. On a few occasions *Enterobacter aerogenes* was isolated, but there was no trace of Type 1 coli. There was no evidence of faecal contamination in the lake.

During the period of the microbial study, a typhoid epidemic broke out at Swansea and a further series of examinations for coliform organisms was made, using the same technique as previously. Samples were taken along the Swansea and Belmont flats close to stormwater drain effluents but no positive results were obtained.

III. Fungi

Rose hips and *Cotoneaster* berries were exposed as baits in wire cages at several stages in Lake Macquarie. Of 200 exposures, four gave positive results. The fungi, identified by Mr. J. T. Waterhouse of Sydney University, included *Trichoderma viride* Persoon ex Fries, *Fusarium* sp. (probably *F. oxysporium* Schlecht), *Aspergillus terreus* Thom, *A. versicolor* (Vuill) Tiraboschi, and a *Penicillium*, probably *P. frequentans* or *P. decumbens*. In addition, a number of *Aspergillus* and *Penicillium* colonies have appeared on agar media inoculated from muds just below water level. They appear to be land forms.

IV. Conclusions

Autotrophic bacteria in Lake Macquarie included all the components of the sulphur cycle, but this cycle was active only in limited areas at certain times, usually during the decomposition of *Zostera* or seaweeds on the flats or close to the shore line. While films of purple sulphur bacteria, *Beggiatoa*, *Thiothrix*, and *Thiovulum* were found in small areas, the green sulphur bacteria were sparse. Carbohydrate digestion by bacteria was at a low level but proteolysis generally was at approximately the same level as reported previously (Wood 1953). Chitin digestion was seasonal but quite high at times.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

V. CHLOROPHYLL DISTRIBUTION

By P. S. Davis*

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Summary

The chlorophyll *a* in samples from five stations in Lake Macquarie was determined over the period July 1955 to November 1956. The mean surface value for the four stations within the lake proper was 1·26 mg/m³. The vertical profile at one station was studied and the mean of these profile values was 1·23 mg/m³. Throughout the period of the survey chlorophyll concentrations in the lake varied from 0·1 to 4·0 mg/m³. The lowest values were found in the late winter and early summer (November) and the peaks during spring and autumn.

The chlorophyll concentration in the surface waters of Lake Macquarie was shown to be significantly higher than that of the marine water entering the lake, but lower than that of a comparison station in the Hawkesbury River.

One series of light penetration measurements made in December 1956 showed that all the water in the lake, and all but one section of Dora Creek, lay within the euphotic zone.

I. Introduction

The objects of the programme were to determine the chlorophyll level in the lake, and to ascertain seasonal variation vertically and horizontally throughout the lake; to use this information to estimate the amount of suspended plant material; to compare the chlorophyll concentrations in the lake with those of the marine water entering the lake; and to obtain data on light penetration in the waters of the lake. As far as possible, collection was done concurrently with the hydrological sampling.

II. Sampling and Stations

Measurements were made from July 1955 to November 1956, at approximately fortnightly intervals. In all, 26 effective surveys were carried out over this period and approximately 300 analyses were made. Detailed results of the analyses will be published elsewhere. The collection of samples on each occasion occupied from a half to nearly two days according to the programme.

The stations at which samples were collected were selected so as to be representative of conditions throughout the lake. Surface water samples were taken at Stations P22, B_2, S18, C_3, W19 (see Spencer 1959, Fig. 1). The vertical profile was studied at Station B_2 by sampling at 2-m intervals to the bottom.

For comparison purposes, a surface water sample was taken at a station on the Hawkesbury River, 13 miles from its mouth.

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III. Methods

(*a*) *Chlorophyll*

A continuous centrifuge was used to concentrate the particulate matter; the plant pigments were extracted with 90 per cent. aqueous acetone, and the chlorophyll *a* measured by its absorption at 665 mμ. This method has been previously described in detail (Davis 1957).

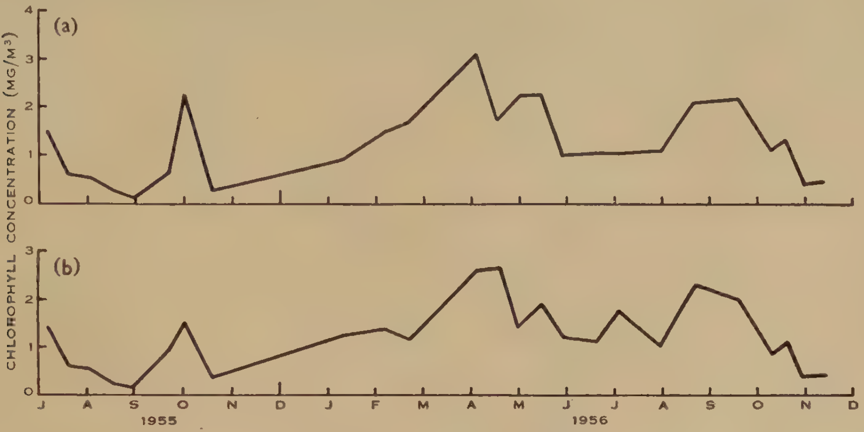

Fig. 1.—Mean chlorophyll values of (*a*) Surface, July 1955–November 1956 (mean of Stations P22, B_2, S18, and C_3); (*b*) vertical profile Station B_2, July 1955–November, 1956.

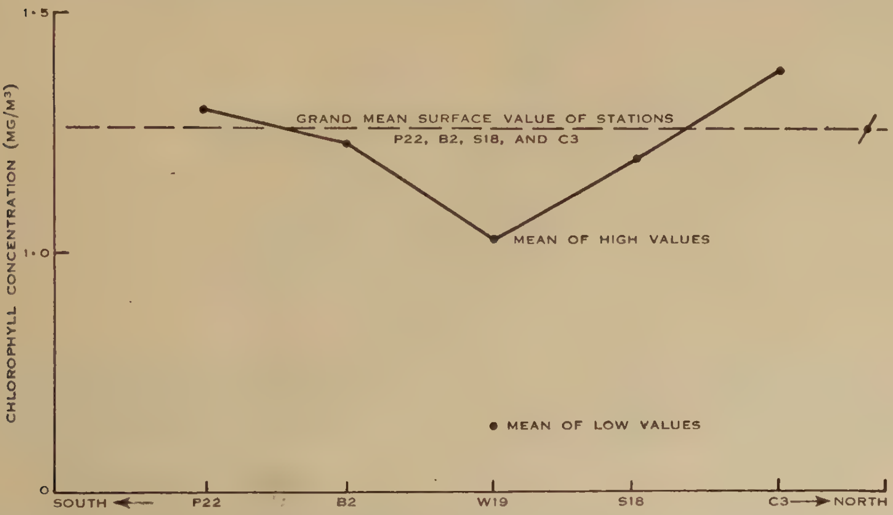

Fig. 2.—Mean chlorophyll values of surface waters at stations from south to north, showing means of high and low values (ebb and flood tide) at Station W19.

(*b*) *Light Penetration*

Light penetration into the lake was measured by means of a submarine photometer fitted with a circular selenium photocell set at the base of a frosted glass diffuser bowl. The instrument has been described by Jitts (1958).

At each station, readings were taken with the submarine photometer just below the surface and then at 1-m intervals to the bottom. The amount of light at each depth was then calculated as a percentage of the light at the surface.

The absorption of light by the water was assumed to be exponential. The logarithms of the percentage of surface light found at the various depths were plotted against depth. The depth to which 1 per cent. of the surface light would penetrate was found by drawing the line of best fit (as judged by eye) through the points of this graph and extrapolating to the 1 per cent. level.

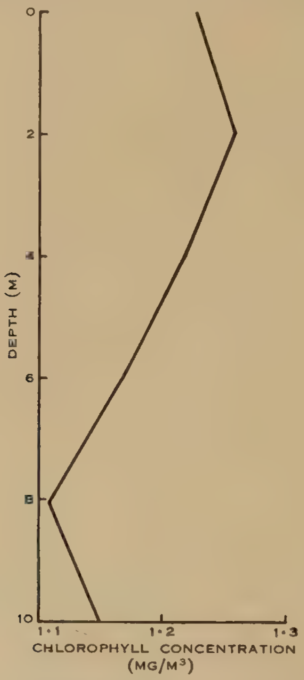

Fig. 3.—Vertical profile of chlorophyll concentration at Station B_2. Means of all samples.

IV. Results

(*a*) *Annual Cycle*

Over the period of the survey, the chlorophyll concentration in the waters of Lake Macquarie varied from 0·1 to 4·0 mg/m³. The mean of all the surface values of Stations P22, B_2, S18, and C_3 was 1·26 mg/m³.

The variation throughout the year of the mean surface values is shown in Figure 1(*a*). The lowest values were found in the late winter and again in early summer (November) after the spring outburst had died off. Chlorophyll peaks were observed during spring and autumn. The highest mean surface value found was 3·1 mg/m³ in April 1956.

In Figure 1(*b*) is shown the annual variation of the mean value of chlorophyll concentration through the vertical profile at Station B_2. It will be seen that the pattern shown here closely follows that of the mean surface values. Furthermore, the mean of all the mean profile values at Station B_2 (1·23 mg/m³), shows no significant difference from the mean of all the surface values of Stations P22, B_2, S18, and C_3 (1·26 mg/m³).

(b) *Horizontal Distribution of Chlorophyll*

In the course of 23 surveys on the lake, surface water samples were collected at Station W19 in the Swansea Channel which is the only exit to the sea. The relationship of the chlorophyll concentration at W19 to the mean surface chlorophyll in the lake depends primarily on whether the W19 sample was collected during an ebb or flood tide.

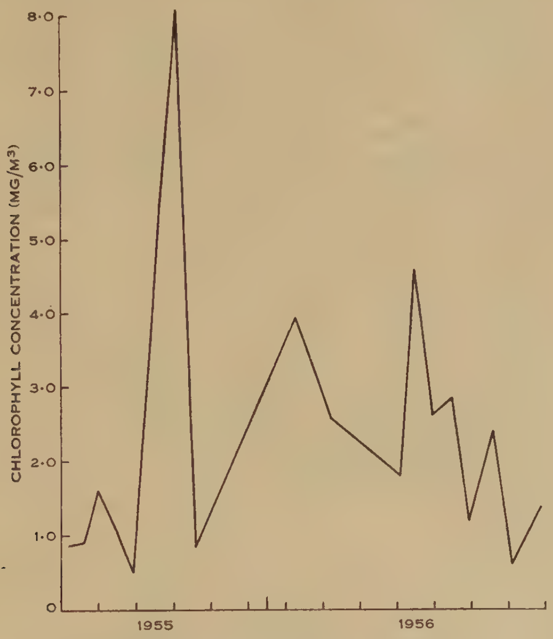

Fig. 4.—Annual cycle of chlorophyll concentration at Hawkesbury River, June 1955–July 1956.

It can be seen from Figure 2 that the chlorophyll concentration in the surface waters of Lake Macquarie is significantly higher than that in the marine water entering the lake. Furthermore, the chlorophyll concentration increases with increasing distance from the channel in either the north or south direction.

(c) *Vertical Profile at Station B_2*

At Station B_2, 23 measurements of the vertical profile of chlorophyll concentration were made. Analysis of the results shows that in general the chlorophyll concentration decreases with increasing depth, but on eight occasions the maximum concentration was found 2 m below the surface.

In 12 of the 23 profiles the minimum chlorophyll value was found at a depth of about 8 m. On these occasions the concentration at 10 m was somewhat higher.

These points are illustrated in Figure 3, where the mean values of all the chlorophyll determinations from each depth at Station B_2 are plotted against depth.

(*d*) *Hawkesbury River*

Over one annual cycle, 19 surface water samples were collected from the station at Hawkesbury River (Fig. 4). The mean chlorophyll concentration was 2·39 mg/m³ in contrast with 1·26 mg/m³ in Lake Macquarie. Furthermore, the Hawkesbury River values show a much greater fluctuation in range than those for Lake Macquarie.

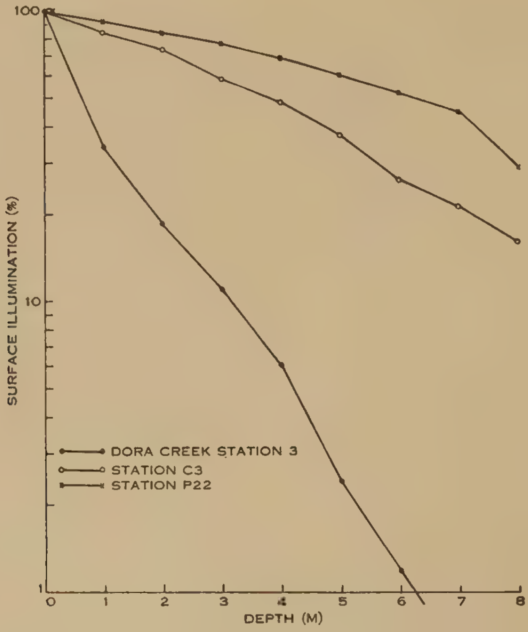

Fig. 5.—Light penetration at three representative stations, Dora Creek 3, C3, and P22.

(*e*) *Light Penetration Measurements*

In December 1956, the light penetration was measured at 12 stations throughout the lake. The results for three representative stations have been plotted in Figure 5. The results show that

(1) There is a great variation throughout the lake and Dora Creek.
(2) There is some evidence that at certain stations (S18, P22, and U26), there is a bottom layer of more turbid water.
(3) The determination of the depth to which 1 per cent. of surface illumination penetrates shows that, at the time of the survey, all the water in the lake lay within the euphotic zone and that except for the deep hole (Station 3) in Dora Creek, sufficient light for photosynthesis should have been available throughout the waters of the lake.

V. Discussion

The mean surface chlorophyll concentration varied from 0·1 mg/m^3 at the end of August 1955 to 4·0 mg/m^3 in early April 1956. The sequence pattern is marked by fairly rapid fluctuations, and the autumn and spring outbursts in 1956 show smaller peaks following the main outburst (Fig. 1(*a*)).

Analysis of the results at Station W19, and comparison of these with the mean values of the surface stations in the lake itself, show that the mean chlorophyll level in the lake is higher than that of the incoming marine water.

There is some evidence, both from high bottom chlorophyll values at Station B_2 and from light penetration measurements, that in some areas the bottom plays an important part in the productivity of the lake. The light penetration measurements show that during December 1956 the whole of the lake bottom was within the euphotic zone.

On the basis of this comparison between Lake Macquarie and the Hawkesbury River, it appears that the mean chlorophyll concentration in a coastal lake is lower than in an open estuary, but is less liable to such great fluctuations in level.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

VI. PLANT COMMUNITIES AND THEIR SIGNIFICANCE

By E. J. F. Wood*

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Summary

There are four plant communities in Lake Macquarie: the sea-grass community, the reef community, the mud bottom community, and the phytoplankton community.

Biologically, the sea-grass community is regarded as being the most important. The epiphytes on the sea-grasses are largely used as food by phytophagous fish and other animals.

The reef community consists of larger brown algae which are not of themselves of great importance, and of felts of blue-green algae such as *Ectocarpus*, and other filamentous forms which are important.

Photosynthetic organisms are sparse in the mud bottoms, except for the tapetic organisms in the sea.

Phytoplankton is relatively abundant.

I. INTRODUCTION

In shallow brackish lagoons such as Lake Macquarie, marine plants are important as food or shelter for the animals. The plant communities were therefore studied during the years 1953–55 as part of the more general programme on the ecology of the lake.

II. METHODS

Observations were made and material collected during monthly surveys of the lake. Material for detailed study of the sea-grass distribution and epiphytic flora was collected by sampling with a 12-in. square turf cutter taking composite samples in each area. The number of stools and leaves of sea-grass per square foot were counted and samples were preserved for enumeration and identification of epiphytes. Preserved samples were shaken violently for 10 min using a mechanical shaker, the sea-grass leaves were removed and weighed, the liquor centrifuged and the wet weight of the epiphytes determined.

Bottom muds were sampled by means of a small grab. Counts were made of the chlorophyll-bearing organisms using a Petroff–Hauser counting chamber under the fluorescence microscope, using the autofluorescence of chlorophyll for the photosynthonts and induced fluorescence with acridine orange for the ciliates and non-photosynthetic flagellates (Wood 1955). The counts were expressed as organisms per gram of mud (wet weight).

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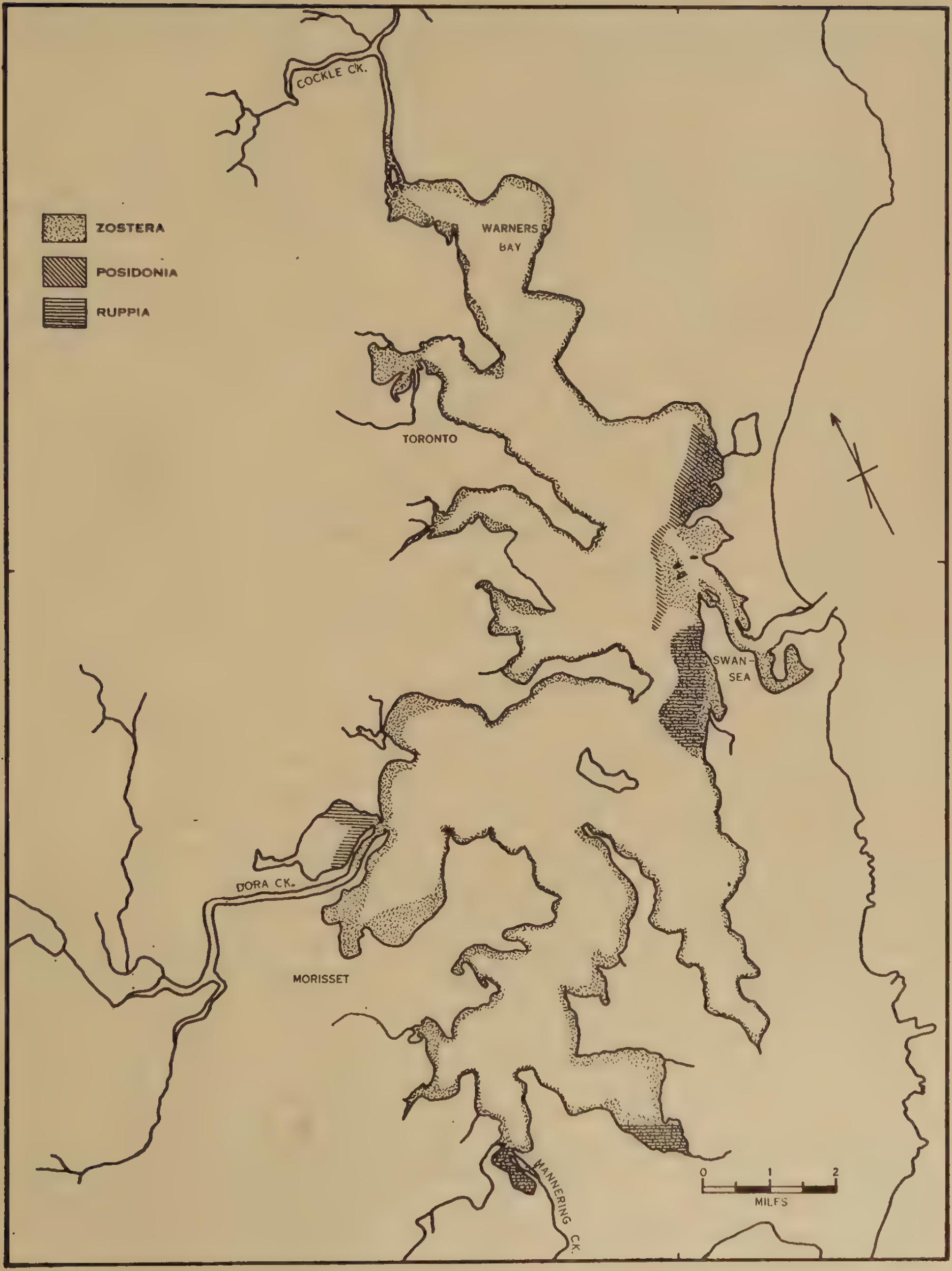
ZOSTERA
POSIDONIA
RUPPIA
COCKLE CK.
WARNERS BAY
TORONTO
SWAN-SEA
DORA CK.
MORISSET
MANNERING CK.
0 1 2
MILES

Fig. 1.—Lake Macquarie, showing the distribution of the sea-grasses.

III. Plant Communities

It is convenient to distinguish four main plant communities in Lake Macquarie: (*a*) the sea-grass community, (*b*) the reef community, (*c*) the mud-bottom community, and (*d*) the phytoplankton community.

(*a*) *The Sea-Grass Community*

(i) *The Sea-Grasses.*—The sea-grasses present in Lake Macquarie include *Zostera capricorni*, *Z. muelleri*, *Posidonia* sp., *Ruppia maritima*, and *Halophila ovalis*. A survey in August 1953 showed that at that time *Zostera* covered 5·4, *Ruppia* 1·8, and *Posidonia* 1·8 square miles of the flats.

Lake Macquarie is almost surrounded by a fringe of *Zostera* of greater or less width, interrupted where the cliffs drop steeply into deep water (Fig. 1). The dominant species was identified as *Z. capricorni*, though *Z. muelleri* was found to be more abundant on a flat near Fennell Bay. *Z. muelleri* in most situations formed a narrow band inshore from *Z. capricorni* but widened to a broad zone on Swansea flat and at Fennell Bay.

In general, growth was more dense in the southern part of the lake than in the north (Fig. 2). The density of the stools varied seasonally, *Z. capricorni* having a minimum density in autumn and winter, whereas *Z. muelleri* is at minimum density in late summer and seems to regenerate in autumn (Fig. 2, Fennell Bay). Growth rate was at a maximum between November and January, and at a minimum in March to April, at which time most leaves of *Z. capricorni* broke off and drifted ashore, forming a bank which was often a foot deep and several feet wide. The flats were almost bare over winter except where *Z. muelleri* appeared. Flowering was most common from October to March, but no seedlings were observed at any time, the annual regeneration apparently being from the stolons in the substrate.

The density of *Zostera* was also locally reduced from time to time by the inroads of swans. In 1953 a very large number of swans, estimated to be between 500 and 1000 at various times, cleared out the *Zostera* from Lake Eraring and in 1955 a similar flock partially bared the Galgabba flats. Swan faeces were collected at this time and found to contain nothing but the partially digested remains of *Zostera* stolons and young shoots. *Zostera* also carpeted the floor of Black Ned's Bay and Dora Creek up to the railway bridge. Part of the entrance channel was also lined with it.

Posidonia was found along the lower part of the flats and extending into the upper part of the slope zone (MacIntyre 1959) between Galgabba and Belmont except opposite the entrance where the sand was in movement. Here the *Posidonia* extended into rather deeper water. In Belmont Bay the *Posidonia* was found in unusually shallow water (about 3 ft deep). *Posidonia* proved to be more permanent than the other sea-grasses as, though many leaves and some plants broke away at the end of each summer, it did not disappear completely from the beds. In shallower water such as in Belmont Bay it was more evanescent. No flowering material was observed in Lake Macquarie so specific identification of the *Posidonia* has not been possible.

Ruppia maritima was the dominant sea-grass in the backwaters and lagoons such as Lake Erraring and Muddy Lake. On Galgabba flats, especially near the discharge of Galgabba Creek, *Ruppia* was found growing through the ground cover of *Zostera capricorni*. This unusual fasciation may be due to the discharge of the creek, on the banks of which is a rich rain-forest flora. The *Ruppia* flowered in November and December and broke away at the end of summer.

Halophila ovalis was never in sufficient quantity to make it an important member of the sea-grass community. It occurred sparsely on Galgabba flats and in deeper water, down to 25 ft, off Myuna Bay, and in Crangan and Chain Valley Bays.

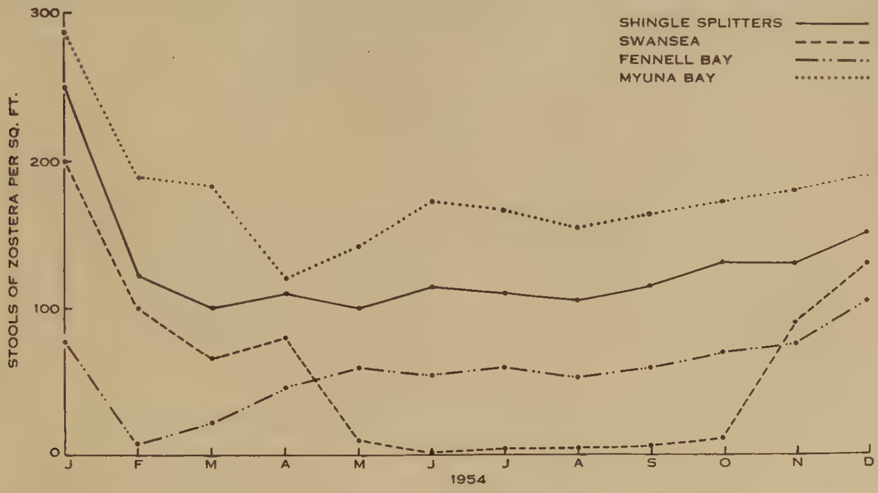

Fig. 2.—Seasonal variation in the stools of *Zostera* per square foot at four points in Lake Macquarie.

(ii) *Environmental Requirements of the Sea-Grasses.*—Only generalities are possible regarding the requirements of the sea-grasses. *Posidonia* was restricted to the Belmont–Galgabba area where the substrate was sandy and with a low organic content, and where sea-water influence was strongest. *Zostera* grew in more reduced environments and extended into more brackish waters than *Posidonia* but in waters less brackish than those where *Ruppia* flourished. *Ruppia* did however occur on the more saline Galgabba flats. J. G. Wood and Baas Becking (1937) have previously recorded *Ruppia* from saline waters. The fact that *Posidonia* and *Zostera* produce reducing substances, but *Ruppia* does not, may be important in their distribution.

The sea-grasses depend for their nutrition on both mud and water, and also contribute materials to these environments by excretion and decay. Their presence indicates great bacteriological activity and considerable variation in pH and redox potential (Baas Becking and Wood 1955). This favours the smaller photosynthetic organisms which have a wide E_h range, i.e. blue-green algae, phytoflagellates, and diatoms. These may be divided into three groups, the organisms of the mud surface, the epiphytic and epontic forms, and the free-living forms growing in close association with the other two groups.

(iii) *The Epiphytes.*—In the sea-grass community there is usually an abundance of small epiphytic or epontic plants attached to the leaf surfaces, to each other, to the thalli of associated algae such as *Cystophyllum*, and to the outside of animals such as molluscs and ascidians. Some species are found on the mud surface having fallen from above or become attached to other material on the bottom. The epiphytes are of great importance in the food chain of the estuary and are most abundant in the sea-grass community. These include a wide variety of algae (Table 1).

Ectocarpus spp. occur as epiphytes on *Zostera* but even more abundantly on the associated alga *Cystophyllum* where they may form a voluminous web which at times traps sufficient oxygen to lift the whole *Cystophyllum* plant with the stone or cockle to which it is attached. The red algae (Rhodophyceae) are found less abundantly on *Zostera* than on the other sea-grasses and *Cystophyllum*.

TABLE 1

THE ALGAL ASSOCIATES IN THE SEA-GRASS COMMUNITY

Cyanophyceae	Phaeophyceae	Rhodophyceae	Chlorophyceae
Oscillatoria	*Ectocarpus* spp.	*Polysiphonia*	*Enteromorpha* spp.
Anabaena		*Ceramium*	*Chaetomorpha*
Nostoc		*Melobesia*	*Cladophora*
Synechococcus			*Vaucheria*
Microcoleus			
Gloeocapsa			

Enteromorpha intestinalis occurs in late winter and early spring, appearing first along the shore-line of shallow, semi-enclosed bays (Whitehead's Lagoon, Fennell Bay) and creeks (Stoney Creek). It develops into dense mats which later break away to become planktonic.

E. prolifera and an unidentified species of *Enteromorpha* begin life as epiphytes but later form free-floating mats in the shallows.

The mat-forming blue-green algae and the colonial diatoms such as *Navicula grevillei* and *Amphipleura micans* frequently form surface felts up to 2 mm thick which bind the substrate. In places such as Swan Bay, Kilaben Bay, and The Hole these felts extend onto the *Salicornia* flats to form a shallow peat. At times the mats lift off and break into clumps which are rolled ashore. Blooms of blue-green algae, *Oscillatoria*, *Anabaena*, *Gloeocapsa*, etc. were present off Cockle Creek and Point Wolstoncroft in October and in May.

Algal blooms of two kinds were distinguished: one is a mixed algal bloom including *Ectocarpus* spp., *Enteromorpha prolifera*, *Enteromorpha* sp. as dominants, with *Ceramium*, *Polysiphonia*, and other filamentous red algae often abundant.

The second type of bloom is composed of *Enteromorpha intestinalis* as a dominant, growing in masses several inches deep, associated with abundant flagellates, blue-green algae, and small gasteropods. The lower portion of this mat may be in contact with reduced mud, and the lower part may be decaying, the centre part dying, and the top still actively growing and reproducing. Both types of algal bloom instigate local sulphate reduction, but the mixed-algal bloom is usually associated with the *Zostera* beds while the *E. intestinalis* bloom generally occurs in the backwaters and creeks.

Epiphytic diatoms occur on the sea-grasses and are extemely important members of the sea-grass community. They are associated with forms which may be entrapped or live intimately within the association, such as *Biddulphia* spp. The species of this community, their prominence in the flora, and their use as fish food as shown by their relative abundance in fish gut, are indicated in Table 2. Their distribution about the lake is shown in Table 3.

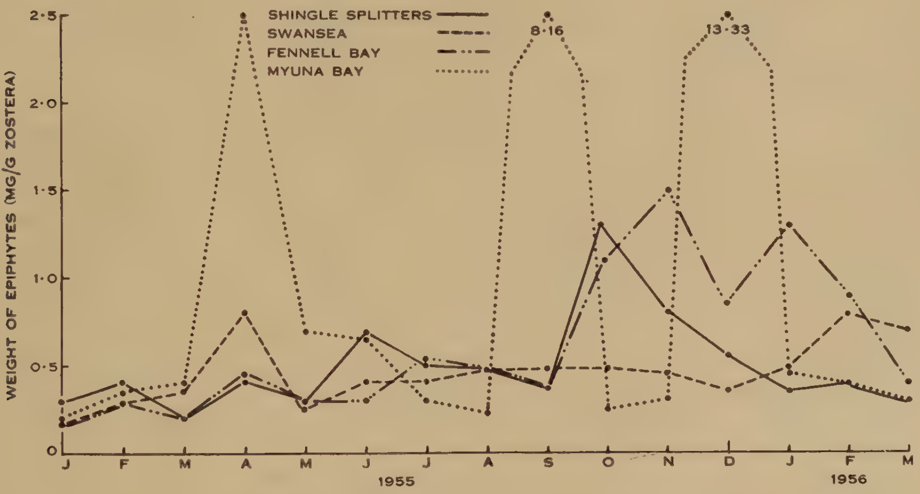

Fig. 3.—Seasonal variation in the weight of epiphytes of *Zostera*.

The densest concentrations of diatoms were in Myuna Bay followed by Dora Creek, Cockle Creek, and Kilaben Bay. Where *Ruppia* was the dominant, sea-grass epiphytes were relatively few.

The diatom population is exemplified by a line transect from Galgabba to Belmont (Table 4). The more abundant forms were widely distributed, for example *Striatella interrupta* occurred at all stations except V. *Cocconeis heteroidea* was absent from the entrance area where marine dominance was greatest. *Synedra* spp. showed their typical uneven distribution, being abundant at stations D and N but not found at neighbouring stations.

The wet weights of epiphytes per gram of *Zostera* at four stations over the seasonal cycle are shown in Figure 3. The stations differ in detail but two maxima, one in late summer and autumn, the other in spring, may be recognized. It should be remembered that these curves represent the residual population after grazing by animals and may depend to some extent on fish movements and seasonal preference. The major peaks in the curve however probably do represent increased algal activity.

TABLE 2

EPONTIC DIATOMS, THEIR SEASONAL OCCURRENCE, AND THEIR RELATIVE IMPORTANCE AS FISH FOOD, CLASSIFIED BY VISUAL ESTIMATION

+, Present; ++, common; +++, dominant; *r*, recorded but rare

Fish examined include mullet, bream, luderick, and leatherjacket

Species	Spring	Summer	Autumn	Winter	Never Dominant	Fish Food
Achnanthes longipes Agardh	*r*	++	*r*	++		+
Amphipleura micans (Lyngbye)	+++			+++		—
Amphora hyalina Kützing	late	++	++	++		+
A. coffaeiformis (Ag.) Kütz.	*r*				+	+
A. javanica A. Schmidt		+	+			+
Bacillaria paxillifer (O.F. Müller) Nitzsch	+++	+++	*r*	*r*		+++
Biddulphia aurita (Lyngbye) de Brebisson					+	+
B. pulchella Gray					+	+
Campylodiscus ornatus Greville					+	+
Cocconeis heteroidea Hantzsch	+++	*r*	*r*	+++		+++
C. scutellum Ehrenberg	++		+			
Diploneis smithii (Breb.) Cleve	+++		++	+++		+
D. crabro Ehr.					+	+
Fragillaria harrisonii (W. Smith) Grunow					+	+
Grammatophora marina (Lyngbye) Kütz.	+++	+++	+++	+++		+++
Hantzschia amphioxys (Ehr.) Grunow					+	+
Licmophora flabellata (Carmichael) Ag.					+	+
L. grandis var. *divisa* (Kütz.) Grunow			+			+
L. abbreviata Lyngbye	+++					+++
Mastogloia cribrosa Grunow	+++	*r*	*r*	*r*		+++
M. quinquecostata Grunow	++ (late)	*r*	*r*	*r*		++
M. strigilis Hustedt	++					—
Melosira moniliformis (Müller) Ag.	++	+	+++	+++		+++
M. sulcata (Ehr.) Kütz.	+	+	+++	+		+++
M. nummuloides (Dillwyn) Ag.				++		++
M. juergensii Ag.	++					+
Navicula cyprinus (Smith) Boyer					+	+
N. brasiliensis Grunow	+++					++
N. grevillei (Ag.) Cleve			+++	+++		+++

TABLE 2 (*Continued*)

Species	Spring	Summer	Autumn	Winter	Never Dominant	Fish Food
Navicula subcarinata Hendey	+++					++
N. yarrensis Grunow					June only	+
N. semen (Ehr.) Donk.		*r*			+	+
N. libellus Gregory		*r*			+	+
Nitzschia closterium (Ehr.) Smith				+++		+++
N. longissima (Breg.) Ralfs					+	+
N. seriata Cleve				+++		—
N. sigma (Kütz.) Smith		+ (Dec.)				—
Pleurosigma angulatum (Queckett) Smith	+	+++	+++	+++		++
P. formosum W. Smith	++	+++	+++			++
P. balticum (Ehr.) Smith					+	+
Striatella unipunctata (Lyngbye) Ag.	+++	+	+++	+		+++
S. interrupta (Ehr.) Heiberg			+++			++
Surirella fastuosa (Ehr.) Kütz.		++				+
Synedra closteroides Grunow					+	+
S. frauenfeldii Grunow	+++					+++
S. fulgens (Grev.) W. Smith		+++	+++	+++		+++
S. ulna (Nitzsch) Ehr.					+	+
Terpsinoe musica Ehr.				++		
Tropidoneis lepidoptera (Greg.) Cleve			++			+
Caloneis excentrica (Green) Boyer		*r*			+	+
Epithemia turgida (Ehr.) Kütz.		*r*			+	+
Pinnularia viridis (Nitz.) Ehr.		*r*			+	+
Rhopalodia musculus (Kütz.) O.F.M.		*r*			+	+
Mastogloia euxina Cleve					+	+
M. brunii mihi (*M. capitata* (Brun) Cleve)					+	+
M. mediterranea Hunt					+	+
M. baldjikiana Green					+	+
M. apiculata W. Smith					+	+

Other forms: *Exuviaella* and *Ceratium*; Cyanophyceae including *Oscillatoria, Lyngbya, Albrightia,* and *Stigonema* (the latter on the brown algae).

TABLE 3

OCCURRENCE OF EPIPHYTIC DIATOMS AND BLUE-GREENS AND DOMINANCE OF DIATOM SPECIES IN LAKE MACQUARIE

M, Moderate; *A*, abundant; *V*, very abundant; *H*, heavy flowering

The numbers record the number of species found. The footnotes record the preponderating species

Location	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Dora Creek 1	1	3	1	$4M^{*}$	$6H^{\mathrm{asi}}$	5	$8H^{\mathrm{bk}}$	$4V^{\mathrm{c}}$	$3V^{\mathrm{g}}$	$6A^{\mathrm{gi}}$	$3M^{\alpha}$	0
Dora Creek 2	$3A^{\mathrm{gn}}$	$2M^{\mathrm{f}}$	0	$8H^{\mathrm{kn}}$	$3M^{\mathrm{v}}$	$3M^{\mathrm{l}}$	$3V^{\mathrm{bk}}$	$2V^{\mathrm{c}}$	$2A^{\mathrm{y}}$	2	2	5
Lake Erraring	2	1	4	$4M^{\mathrm{a}}$	6	0	0	0	1	1	—	4
The Hole	$1M^{\mathrm{j}}$	4	0	$5M^{\mathrm{q}}$	$3M^{\mathrm{v}}$	1	4	$4M^{\mathrm{b}}$	$8M^{\mathrm{e}}$	$4M^{\mathrm{h}}$	—	$4M^{\mathrm{g}}$
Shingle Splitter's Pt.	$7M^{\mathrm{p}}$	4	4	—	$3M^{\mathrm{m}}$	0	$4M^{\mathrm{b}}$	$5M^{\mathrm{d}}$	3	2	—	$2A^{\mathrm{hv}}$
Whiteheads Lagoon	4	—	6	$4A^{\mathrm{fj}}$	—	—	$5H^{\mathrm{bk}}$	$6A^{\mathrm{dh}}$	$6A^{\mathrm{mz}}$	3	2	0
Myuna Bay	$5M^{\mathrm{d}}$	0	4	10	—	4	$4H^{\mathrm{wx}}$	0	1	$8H^{\mathrm{gi}}$	$10H^{\mathrm{av}}$	$7H^{\mathrm{alfv}}$
Wangi South	2	0	1	$7A^{\mathrm{fj}}$	3	1	1	3	1	2	2	0
Wangi North	6	0	0	2	2	4	6	$4V^{\mathrm{b}}$	$7M^{\mathrm{l}}$	3	0	4
Kilaben Bay	3	$8H^{\mathrm{a}}$	—	3	7	$5M^{\mathrm{a}}$	7	$8H^{\mathrm{gdmf}}$	3	$1M^{\mathrm{h}}$	7	0
Fennell Bay	2	0	$4M^{\mathrm{c}}$	0	$7M^{\mathrm{h}}$	5	$3H^{*\mathrm{x}}$	$1M^{\mathrm{m}}$	5	$4M^{\mathrm{o}}$	$3A^{*}$	1
Cockle Creek 1	5	4	0	$5M^{\mathrm{l}}$	0	4	$6H^{\mathrm{bp}}$	8	2	0	1	$6H^{\mathrm{al}}$
Cockle Creek 2	1	0	6	$3M^{\mathrm{a}}$	0	1	$6A^{\mathrm{d}}$	—	$6H^{*\dagger}$	H^{*}	2	0
Belmont	$5M^{\mathrm{a}}$	0	10	—	$6M^{\mathrm{u}}$	$3V^{\mathrm{k}}$	5	$4M^{\mathrm{b}}$	2	$10M^{\mathrm{r}}$	$8M^{*}$	0
Swansea	$6M^{\mathrm{a}}$	2	2	6	$5V^{\mathrm{t}}$	$7M^{\mathrm{a}}$	1	5	4	0	2	$6M^{\mathrm{l}}$
Stony Creek	—	0	1	3	0	—	—	$6V^{\mathrm{hx}\beta}$	$3M^{\mathrm{g}}$	—	6	—

[a] *Synedra fulgens*
[b] *Cocconeis heteroidea*
[c] *Cocconeis scutellum*
[d] *Grammatophora marina*
[e] *Mastogloia strigilis*
[f] *Pleurosigma formosum*
[g] *Synedra frauenfeldii*
[h] *Striatella unipunctata*
[i] *Licmophora abbreviata*
[j] *Amphora javanica*
[k] *Navicula grevillei*
[l] *Amphora hyalina*
[m] *Melosira moniliformis*
[n] *Pleurosigma angulatum*
[o] *Amphora pellucida*
[p] *Achnanthes longipes*
[q] *Melosira sulcata*
[r] *Navicula granulata*
[s] *Nitzschia closterium*
[t] *Terpsinoe musica*
[u] *Tropidoneis lepidoptera*
[v] *Bacillaria paxillifer*
[w] *Diploneis smithii*
[x] *Mastogloia cribrosa*
[y] *Melosira nummuloides*
[z] *Navicula subcarinata*
[α] *Nitzschia sigma*
[β] *Melosira juergensii*

*Blue-green algae. †*Cladophora*, *Ectocarpus*, *Chaetomorpha*.

TABLE 4

DISTRIBUTION OF EPIPHYTIC DIATOMS FROM GALGABBA POINT TO BELMONT

A to K at 1-yd intervals; L to P at 100-yd intervals; Q to V at 400-yd intervals

P, present; *C*, common; —, absent

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
Striatella interrupta	*C*	*C*	*P*	*C*	*P*	*P*	*P*	*C*	*P*	*P*	*C*	*P*	*P*	*P*	*P*	*P*	*C*	*P*	*P*	*P*	*P*	—
Biddulphia aurita	*P*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*
Cocconeis heteroidea	*P*	*C*	*C*	*P*	*C*	—	*P*	*P*	*P*	*P*	—	*P*	*P*	—	—	—	—	—	—	*P*	*P*	—
Pleurosigma formosum	*P*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—
Amphora javanica	*P*	—	—	—	—	—	—	*P*	—	—	*P*	—	—	—	—	—	—	—	—	—	—	—
Melosira moniliformis	*P*	—	*P*	*P*	—	*P*	*P*	*C*	—	—	*P*	*P*	*P*	—	*P*	—	—	—	—	*P*	—	—
Pleurosigma angulatum	*P*	—	—	*P*	—	*P*	—	*P*	*P*	*P*	—	*P*	*C*	*P*	*P*	—	—	—	—	—	—	—
Mastogloia quinquecostata	*P*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	*P*	*P*	*P*	—	—
Melosira sulcata	*P*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	*P*	—	—	—	—
Trachyneis aspera	*P*																					
Grammatophora marina	—	—	*P*	—	—	—	—	—	—	—	—	*P*	*C*	*P*	—	—	—	—	—	—	*P*	—
Synedra frauenfeldii	—	—	*P*	*P*	*P*	*P*	—	*P*	—	—	—	—	—	*C*	—	—	*P*	—	—	—	—	—
Licmophora abbreviata	—	—	—	*C*	—	—	—	—	—	—	*P*	—	*P*	*C*	—	—	—	*P*	—	—	*P*	—
Synedra fulgens	—	—	—	*C*	—	—	—	—	—	—	—	*C*	—	—	—	—	—	*C*	—	—	—	—
Striatella unipunctata	—	—	—	*P*	—	*P*	—	*P*	—	—	—	—	*P*	—	—	—	—	—	—	*P*	—	*P*
Synedra closteroides	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—	—	—	—	*P*	*P*	—
Licmophora flabellata	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—	—	—	—	—
Licmophora divisa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—	—	—	—
Navicula granulata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—	—	—	—
Surirella fastuosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	*P*	—	—	—	—
Navicula subcarinata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—	—	—	—	—
Plagiogramma distans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—
Amphora hyalina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*	—	—
Diploneis crabro	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*P*

The flora of the mud substrate around the sea-grasses (Table 5) is distinct from the epiphytic flora.

Table 5

DIATOMS AND BLUE-GREEN ALGAE OCCURRING IN MUDS OF SEA-GRASS FLATS

DIATOMS

Dominant Species
Nitzschia closterium (Ehr.) W. Smith: Dora Ck. (May)
Navicula grevillei (Ag.) Cleve: Cape Wolstoncroft (Aug.)
Amphipleura micans (Lyngbye): Myuna (June, Aug.)

Common Species (Subdominant)
Diploneis smithii (Breb.) Cleve: Lake Erraring (Mar.)
Synedra fulgens (Grev.) W. Smith: Kilaben Bay (May)
Mastogloia cribrosa Grunow: Fennell Bay (Nov., Dec.), Cockle Ck., Belmont (May)
Synedra frauenfeldii Grunow: Dora Ck. (May)
Cocconeis heteroidea Hertz.: Wangi (Aug.), Dora Ck., Fennell Bay, Cockle Ck. (July), Belmont (Aug.)

Species Present, Never Dominant
Navicula subcarinata Hend.
Synedra ulna (Nitz.) Ehr.
Melosira juergensii Ag.
Licmophora grandis var. *divisa* (Kütz.) Grunow
Grammatophora marina (Lyngbye) Kütz.
Licmophora abbreviata Ag.
Striatella unipunctata (Lyngbye) Ag.
Pleurosigma formosum W. Smith
Surirella fastuosa (Ehr.) Kirby
Mastogloia quinquecostata Grunow
Bacillaria paxillifer (O.F.M.) Angsch.
Melosira moniliformis (Müller) Ag.
Pleurosigma balticum (Ehr.) W. Smith
Campylodiscus ornatus Grev.
Pleurosigma angulatum (Queckett) W. Smith
Terpsinoe musica Ehr.
Hantzschia amphioxys (Ehr.) Grunow
Mastogloia cribrosa Grunow
M. gracilis Humboldt
M. smithii Thwaites
M. cocconeiformis Grunow
Amphora hyalina Kütz.
Biddulphia aurita (Lyngbye) Breb.
Melosira sulcata (Ehr.) Kütz.
Navicula lyra Ehr.
N. lyra var. *elliptica* A. Sch.
N. cyprinus (W. Smith) Boyer var. *australica* A. Sch.
N. granulata—brasiliensis Grunow
N. peregrina (Ehr.) Kütz.
Amphora javanica A. Sch.
Achnanthes longipes Ag.
Diploneis crabro Ehr.
Auliscus sculptus (W. Smith) Ralfs
Tropidoneis lepidoptera (Greg.) Cleve
Triceratium alternans Bail.
Trachyneis aspera (Ehr.) Cleve
Amphora granulata Greg.
Auliscus punctatus Bail.
Pinnularia major W. Smith
Amphiprora alata (Ehr.) Kütz.
Nitzschia hungarica Grunow
Surirella gemma (Ehr.) Kütz.
Amphora gigantea Grunow
A. ostrearia Breb.
Diploneis fusca (Greg.) Cleve

BLUE-GREEN ALGAE

Oscillatoria sp.
Lyngbya spp.
Microcoleus spp.

(b) *The Reef Community*

The reef community of Lake Macquarie forms a narrow fringe below low water on the steeper rocky shores. Shallow reefs occupy considerable areas off Shingle Splitter's Point and south to Bird Cage Point, off Wangi, and in broken patches in the Speer's Point–Toronto section.

Attached to rocky outcrops and shores are to be found a number of algae, e.g. *Sargassum* spp., *Cystophyllum muricatum* Ag., *Cystophora*, *Dictyota* spp., and *Codium* spp., including *C. pomoidea* Ag. and *C. lucasi* Setch. The epiphytic flora is not as dense as that of *Zostera* and the algae themselves occur in clumps or bands (attached at a particular level or to a particular stratum of rock). The density of attachment of epiphytes depends on the texture of the host surface; for example, *Cystophyllum*, no doubt on account of the glandular nature of its surface, is frequently covered with epiphytes, usually *Ectocarpus* or blue-green algae. Many of the Sargassaceae will be found attached to such material, and thus the shingle areas in the northern part of the lake may in part be assigned to the reef community. The mussel *Trichomya* is frequently associated with the Sargassaceae. The smaller forms which dominate the reef community include green and blue-green algae in the intertidal zone—here restricted to a few inches—and brown and red algae below.

The green algae include *Chaetomorpha*, *Enteromorpha*, and *Vaucheria*; the blue-greens *Nostoc*, *Anabaena*, and *Gloeocapsa* in fresh and brackish water, and *Merismopedia*, *Microcoleus*, *Amphithrix*, and *Albrightia* when the salinity is somewhat higher. The red algae include *Polysiphonia*, *Ceratium*, and *Melobesia*, while the dominant brown is *Ectocarpus*.

In sheltered areas, the blue-greens often form a felt covering the rocks. They are easily scraped off, owing to the presence beneath them of a reduced layer of black mud containing *Desulphovibrio* and, often, purple and green sulphur bacteria. The presence of these organisms can be demonstrated by placing a portion of the felt in a glass cylinder, when the smell of hydrogen sulphide will soon become manifest; *Desulphovibrio* can be isolated on lactate media; and purple *Chromatia* and green *Chlorobia* soon appear at the side of the cylinder below the blue-greens.

In the field, the E_h of the black mud is of the order of -200 mV and that of the water above the felt of blue-greens is of the order of $+450$ mV in the day-time. There is laboratory evidence that these organisms can photoreduce when growing at E_h values of -170 to -240 mV (Frenkel 1949; Baas Becking and Wood 1955). The latter authors have shown that the blue-green algae can occupy the low pH–E_h range of the purple and green sulphur bacteria.

(c) *Mud Bottom Community*

The mud bottoms of Lake Macquarie, though largely within the photic zone, are relatively inactive. Very few photosynthetic plants occur, and bacterial activity is slight. There are a few photosynthetic flagellates, very few non-photosynthetic flagellates, and some ciliates (see Table 6). In some 400 samples of bottom muds, no actively multiplying cells of the photosynthonts were observed, whence it is concluded that most of these organisms found on the mud surface were allochthonous.

(d) *The Phytoplankton Community*

The phytoplankton community consists of diatoms, dinoflagellates, small naked flagellates, occasionally *Chlorella*, silicoflagellates, and coccolithophores.

TABLE 6

MICROORGANISMS OF THE MUD SURFACE OBSERVED BY FLUORESCENCE MICROSCOPY

Numbers per gram of wet mud

+, present; ++, common

Station	Diatoms	Flagellates	Ciliates	Blue-Greens	Bottom
Marmong Pt.	—	—	—	—	Coarse gravel
South Ck.	+	+	—	+	Sandy mud with decomposed *Zostera*
Myuna Bay (1955)	+	+ (some colourless)	—	—	Fine sand and gravel
(1956)*A*	1×10^6	1×10^6	11×10^6	—	Mud
(1956)*B*	—	$<5 \times 10^4$	—	—	Mud and H_2S
Wyee (The Hole)	+	+ (colourless)	+	—	Black mud
Fennell Bay (1956)*A*	+	+	—	—	Gravel
B	5×10^5	5×10^5	—	—	Sand
Shingle Splitter's Pt. (1956)*A*	++	+	—	—	Fine gravel
(1956)*B*	—	2×10^5	1×10^5	—	Mud and H_2S
(1956)*C*	—	2×10^5	1×10^5	—	Sand
Swansea flats, *A*	++	+	—	—	Fine gravel
B	2×10^6	2×10^5	1×10^5	—	Sand (nematodes)
Belmont flats, *A*	+	+	—	—	Sandy mud
B	—	3×10^5	—	—	Sand
Cockle Ck.	—	1×10^4	—	—	Sand
Deep Stations					
Shingle Splitter's Pt.	—	5×10^4	—	—	Blue mud
Coal Pt.	—	$<5 \times 10^4$	—	—	Blue mud
Wangi, *A*	—	$<5 \times 10^4$	—	—	Black mud
B	—	$<5 \times 10^4$	—	—	Black mud

(i) *Diatoms.*—The diatom usually dominant throughout the investigation in the lake is the normally oceanic *Chaetoceros peruvianum* but there appears to have been a decline in the abundance of this form, especially in 1955 to 1956. Such a decline of the dominant form has been recorded by Wood (1954) among dinoflagellates.

Three diatom blooms were recorded in 1955 in January, in April, and the major (spring) bloom in August (see Fig. 4). During each of these, oceanic diatoms appeared at the entrance, Pelican Island, Coal Point, and Mark's Point, indicating that the oceanic influence extends, at times, along the eastern shore of the lake to the north and across to Coal Point on the western side. Bacterial counts for April 1956 at Pelican Island and Coal Point confirm this to some extent (Wood 1959).

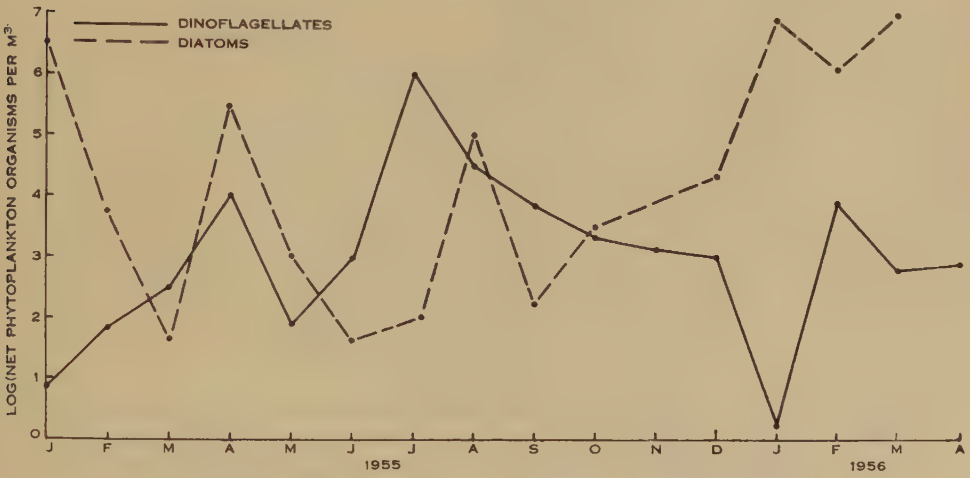

Fig. 4.—Seasonal variation of phytoplankton in Lake Macquarie.

Skeletonema costatum has a fresh to brackish water habitat in Lake Macquarie, and is characteristic of Cockle Creek, but has been found in the lake on only two occasions, at Wangi in May 1955, and off Green Point in September 1953.

There is no evidence of oceanic influence on the phytoplankton in the lake south of the entrance channel. The planktonic diatoms, which have been recorded, are listed in Table 7.

(ii) *Dinoflagellates.*—In Lake Macquarie, the dinoflagellates are almost entirely confined to the plankton, exceptions being *Exuviaella* and several species of *Gymnodinium*, which occur in the *Zostera* flats. The largest populations and the greatest number of species are to be found off Pelican Island, where the lake and ocean waters mix. Speaking generally, the dinoflagellates are commonest in the central portion of the lake from Shingle Splitter's Point to Croudace Bay, and less prolific in the Mark's Point region, in Dora Creek, off Coal Point, and, except when fresh water influence is strong, in Cockle Creek. Cockle Creek has, at such times, a large concentration of *Peridinium minutum*, and a minute, hyaline *Goniaulax* (Wood 1954, Fig. 180). At times there is evidence of an invasion by marine forms, exemplified by *Peridinium globulus*, *P. claudicans*, *Ceratium massiliense*, etc. These forms occur rarely, but spread over the lake, with the greatest concentration near the entrance, as would be expected. Some species usually regarded as oceanic or oceanic–neritic are endemic in Lake Macquarie, e.g. *Pyrophacus horologicum*, *Peridinium depressum*, *P. brochi*.

TABLE 7

PLANKTONIC DIATOMS OF LAKE MACQUARIE

Chaetoceros peruvianum Brightwell
C. teres Cleve
C. danicum Cleve
C. lorenzianum Grunow
C. sociale Lauder
C. concavicorne Mangin
C. decipiens Cleve
C. secundum Cleve
Coscinodiscus centralis Ehr.
C. centralis var. *pacifica* (Gran & Angst)
C. granii Gough
C. concinnus W. Smith
C. excentricus Ehr.
Guinardia flaccida (Castracane) Peragallo
Hemiaulus sinensis Grev.
Stephanopyxis turris (Grev. & Arnot) Ralfs
S. palmeriana (Grev.) Grunow
Streptotheca thamesis Shrubsole
Schroederella delicatula (Peragallo) Pavillard
Rhizosolenia alata Brightwell
R. stolterforthii Peragallo
R. setigera Brightwell
R. styliformis Brightwell
R. robusta Norman
R. calcar-avis Schultze
Bacteriastrum delicatulum Cleve
Melosira moniliformis (Müller) Ag.
M. sulcata (Ehr.) Kützing
M. juergensii Ag.
M. nummuloides (Dillwyn) Ag.
Eucampia zoodiacus Ehr.
Ditylum brightwellii (West) Grunow
Thalassiosira rotula Meunier
T. subtilis (Ostenfeld) Gran
Skeletonema costatum (Grev.) Cleve
Hyalodiscus stelliger Bailey
Auliscus sculptus (W. Smith) Ralfs
Biddulphia pulchella Gray
B. aurita (Lyngbye) Breb.
B. turgida (Ehr.) W. Smith
Corethron criophilum Castracane
Asteromphalus flabellatus (Breb.) Grev.
Leptocylindrus danicus Cleve

The dominant species in the phytoplankton are *Ceratium buceros*, *C. furca*, *Peridinium divergens*, *P. depressum* as regular members, and *Dinophysis caudata*, *Prorocentrum micans*, *Goniaulax monacantha*, *G. spinifera*, *G. digitale*, *G. diegensis*, *Peridinium roseum*, and *Pyrophacus horologicum* as irregular dominants.

During the period of observation, dinoflagellates have occurred in blooms in July–August, and in 1954 there was a peak in January which was not repeated in 1955, but appeared in February 1956 (see Fig. 3). Generally speaking, blooms of the diatom *Coscinodiscus* and of dinoflagellates coincided, the main dinoflagellate at such times being *Ceratium buceros*. On occasions, e.g. in November 1953, the dinoflagellates outnumbered the diatoms in the plankton.

The species recorded are listed in Table 8.

IV. Microorganisms in the Food Chain

The observations made during this investigation show that the sea-hare *Aplysia*, the bream *Mylio australis* (Gunther), and the garfish *Reporhampus ardelio* (Whitley) eat, and appear to digest, *Zostera* tips, since these were repeatedly found in the stomach, and were considerably eroded as they reached the hind gut. The gasteropod *Pyrazus* was found to ingest diatoms, more especially stipitate, epontic forms, which normally occur on *Zostera*. Mullet and bream stomachs also contained epontic forms including the algae *Cladophora*, *Ectocarpus*, and *Chaetomorpha*, and diatoms such as *Licmophora*, *Synedra*, *Striatella*, *Pleurosigma* spp., *Grammatophora*, *Melosira*, and *Cocconeis*. Bream is regarded as a carnivore, but frequently the stomachs contained a considerable amount of plant material. The relative importance of diatom species and algae as fish food is indicated in Table 2. It will be seen that epontic diatoms are consumed by phytophagous fish throughout the year, while blue-green algae and dinoflagellates only appeared in fish stomachs in spring and summer. In the winter, fish feeding in Stoney and Stockton Creeks were feeding on *Cladophora*, *Chaetomorpha*, and other epontic algae rather than diatoms. Stomachs of bream (*Mylio australis*) were found to contain diatoms, including *Cocconeis heteroidea*, *Pleurosigma angulatum*, *P. formosum*, *Melosira moniliformis*, *Striatella unipunctata*. Small mullet of various species and young bream were also found to ingest these and other diatom species. The presence in fish stomachs of *Biddulphia* and *Nitzschia longissima* suggests that the fish derive food from the water of the *Zostera* flats as well as from the epiphytes, but that the latter are by far the most important. The presence of *Hantzschia amphioxys*, and *Fragilaria harrisonii* in fish stomachs suggests either strong fresh water influence in the lake at the time or that the fish had recently come down from the creeks.

It was frequently observed that the diatom flora of the fish stomachs corresponded to that of other parts of the lake than that in which the fish were caught. Table 4 shows that the dominant species are reasonably constant over an area of flat, and that the subdominants vary from place to place. It would appear, then, that fish movements may be indicated by a study of the littoral epontic flora and the flora of fish stomachs. Table 9 shows the degree of correspondence between the diatoms of the *Zostera* association, mud surface, and mullet stomachs (see also Crosby and Wood 1959). It will be seen from the two cases given that the stomach

TABLE 8

SPECIES OF DINOFLAGELLATES RECORDED FROM LAKE MACQUARIE

Phalacroma lens Kofoid & Skogsberg.	Frequent, never common.
P. ovum Schütt.	Rare.
Dinophysis caudata Saville Kent.	Frequent and common.
D. tripos Gourret.	Rare.
D. okamurai Kofoid & Skogsberg.	Rare.
D. fortii Pavillard.	Occasional, but may be dominant.
D. sacculus Stein.	Rare.
D. diegensis Kofoid.	Rare.
D. ovum Schütt.	Rare.
Exuviaella compressa (Bailey) Ostenfeld.	Rare.
Prorocentrum micans Ehr.	Often numerous, never dominant.
P. scutellum Schroeder.	Rare.
Pyrophacus horologicum var. *steinii*.	Numerous, at times semidominant.
Diplopsalis lenticula Bergh.	Frequent, not common. (Var. *minor* Paulsen, rare.)
Peridinium divergens Ehr.	Frequent, often dominant.
P. depressum Bailey.	Frequent, may be subdominant.
P. minutum Kofoid.	Frequent and common at times in Cockle Creek region.
P. leonis Pavillard.	Rare.
P. roseum Paulsen.	Very numerous at times.
P. granii Ostenfeld.	Rare.
P. pellucidum (Bergh) Schütt.	Rare.
P. solidicorne Mangin.	Rare.
P. ovum Schiller.	Rare.
P. globulus Stein.	Rare.
P. thorianum Paulsen.	Rare—common April 1955.
P. pentagonum Gran.	Infrequent but may be numerous.
P. conicum (Gran) Ostenfeld & Schmidt.	Infrequent.
P. brevipes Paulsen.	Rare.
P. cerasus Paulsen.	Infrequent but may be fairly numerous.
P. pentagonum var. *latissimum* (Kofoid) Schiller.	Not common.
P. brochii Kofoid & Swezy.	Rare.
P. abei Paulsen.	Rare.
P. ovatum (Pouchet) Schütt.	Rare.
P. steinii var. *mediterraneum* Kofoid.	Moderate.
P. pedunculatum Schütt.	Rare.
P. claudicans Paulsen.	Frequent but not common.
P. ventricum Abe.	Rare.
P. ampulliforme Wood.	Rare.
Protoceratium reticulatum (Claparède & Lachmann).	Rare.
Goniaulax spinifera (Claparède & Lachmann) Diesing.	Common.
G. diegensis Kofoid.	Frequent but not common.
G. digitale (Pouchet) Kofoid.	Common and frequent.
G. monacantha Pavillard.	Frequent and common.
G. polygramma Stein.	Frequent.
G. alaskensis Kofoid.	Rare.
G. diacantha (Meunier) Schiller.	Rare.
G. sp. (Wood 1954, Fig. 180).	Common Cockle Creek area.
G. minima Matzenauer.	Relatively common at times.

TABLE 8 (*Continued*)

G. polyedra Stein. Rare; recorded from Dora Creek only.
G. scrippsae Kofoid. Very rare.
Ceratium buceros (Zacharias) Schiller. Usually dominant.
C. furca (Ehr.) Claparède & Lachmann. Very common and frequent.
C. fusus (Ehr.) Dujardin. Common at times.
C. minutum Jørgensen. Rare.
C. massiliense (Gourret) Jørgensen. Rare.
C. tripos (O. F. M.) Nitzsch. Somewhat rare.
forma *tripodioides* (Jørgensen) Paulsen. Somewhat rare.
C. breve (Ostenfeld & Schmidt) Schroeder. Mark's Point on 2.iv.55. Present on 18.iv.55 off Jibbon (oceanic).

TABLE 9

COMPARISON OF DIATOM FLORAS FROM MULLET STOMACHS WITH THOSE OF MUDS AND ZOSTERA

The number indicates the number of fish containing the species

P, Present; *C*, common; *D*, dominant; —, absent

Species	Series *A*			Series *B*		
	Mullet	*Zostera*	Mud	Mullet	*Zostera*	Mud
Climacosphenia moniligera	7*C*	*C*	—			
Licmophora flabellata	*C*	—	—	—	*P*	—
Navicula brasiliensis	8*D*	*D*	*C*	—	*P*	—
Striatella unipunctata	1*P*	*C*	*P*	6*C*	*C*	—
Synedra frauenfeldii	—	—	*P*	2*C*	*P*	*P*
Navicula subcarinata	4*P*	*P*	—	—	*P*	*D*
Auliscus sculptus	4*P*	*P*	*P*	—	—	*P*
Biddulphia aurita	9*P*	*P*	*P*	—	*P*	*P*
Diploneis smithii	3	*P*	*P*			
Triceratium alternans	1*P*	—	*P*			
Tropidoneis lepidoptera	1*P*	—	*P*	1*P*	—	*P*
Melosira sulcata	4*P*	—	—			
Navicula lyra var. *elliptica*	1*P*	—	—	—	—	*P*
N. grevillei	1*P*	—	—	—	*P*	—
Licmophora abbreviata	—			5*D*	*D*	*P*
Amphora granulata	—	—	—	1*P*	—	*P*
A. hyalina				—	—	—
Bellerochea malleus	3*P*	—	—			
Trachyneis aspera				—	—	*P*
Achnanthes longipes				—	*P*	—

flora corresponds more closely to that of the *Zostera* than to that of the mud. This was found to be the case in most instances where any correspondence could be observed. In some cases, the stomach flora corresponds to that of adjacent areas rather than to the areas in which the fish were caught, while in other cases the stomach flora was unlike that of any of the collecting stations.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

VII. THE BENTHIC MACROFAUNA

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Summary

The benthic zone of Lake Macquarie, passing from shallow to deep water, consists of weed, slope, and mud zones, occupying respectively 23·5, 16·0, and 60·5 per cent. of the lake area. The biomasses of the invertebrate macrofauna of the zones are respectively 94±56 g, 180±12 g, and 10·6±9·4 g per m^2. Each zone has its typical fauna. A variety of species occurs in the weed and slope zones, but only two species occur in number in the mud zone.

A number of mollusc species was represented only by dead shells of recent origin, suggesting some catastrophe such as production of anaerobic conditions. There is no evidence that the mussel *Trichomya hirsuta* was affected, and experimentation revealed that this species can survive long periods of immersion under anaerobic conditions.

I. INTRODUCTION

The benthic macrofauna was investigated to determine what quantities and types of these organisms existed in the lake, and to ascertain their distribution and the relation of the faunal distribution to the nature of the substrate.

II. METHODS

The survey was conducted from a launch fitted with an electric winch, which hauled a wire cable attached either to a 12-in. triangular dredge fitted with a coarse mesh net for qualitative work or a 0·1 m^2 Van Veen grab for quantitative work. At the beginning of the survey self-contained diving apparatus was used to check by visual inspection the adequacy of the dredge samples. As no discrepancies were noted this procedure was discontinued in later stages of the survey.

The Van Veen grab was found to work efficiently on muddy areas, but on hard sand or bottoms with abundant shell, stone, or weed it was unsatisfactory. On shallow weed-covered flats, a cylinder of 0·1 m^2 cross-sectional area was pushed into the bottom and the contents later scraped out.

On the slope area between the shallows and the mud substrate of the deep lake bottom, neither method was practicable. To sample this area, a fine mesh bag was tied over the top end of the cylinder, and an aqualung diver pushed the cylinder as far as possible into the bottom, then inverted it to transfer the contents to a bag. Five samples were taken at the majority of stations.

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* Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, N.S.W.

Samples were washed and sorted through sieves, the finest of which had 14 meshes to the square inch; they were stored in formalin and later weighed by a standard method of damp-drying with filter paper.

The stations mentioned in the text are shown in Spencer (1959, Fig. 1).

III. ECOLOGICAL ZONATION

The entrance channel is quite distinct from the rest of the lake. The bed of the lake itself can be divided into three zones: a weed zone extended from the shore to a depth of 3 or 4 m, a mud zone occupying the almost flat lake bottom at depths of 7 to 10 m, and an intermediate zone with distinct biological characteristics. The boundaries of these zones are more sharply defined on steep shores than in those more gently inclined.

Some 400 stations were occupied in the lake proper, and from these the zonal distribution of the bottom types was mapped and the relative areas of each estimated by cutting and weighing the areas of the map. The method had a standard error of 2·8 per cent. for 19 standard mile squares. The total area of 41·84 sq. miles is divided as follows:

Weed zone:	9·84 sq. miles	= 23·5 per cent.
Slope zone:	6·66 sq. miles	= 16·0 per cent.
Mud zone:	25·34 sq. miles	= 60·5 per cent.

(*a*) *The Entrance Channel*

The sandy floor of the entrance channel is practically barren, presumably owing to the abrasive action and movement of the sand during the tidal flow. The rock walls bounding much of the channel support a typical intertidal fauna as described by Dakin (1952, Chapter IX). As this zone is considered to provide little of the bottom-living food of the lake fish, no further consideration is given to it.

(*b*) *The Weed Zone*

Within the lake where there is practically no tide, the normally intertidal species, such as the oyster *Crassostrea commercialis*, are restricted to a narrow band a few inches wide at the upper edge of the weed zone wherever rock provides a suitable substrate. In the weed zone the substrate is in places rocky or pebbly; in others sandy with varying admixtures of mud.

Dominant in this zone are the sea-grasses or, on rocky shores, such larger algae as *Cystophyllum* and *Codium*. They provide the habitat of many organisms, and provide a nursery area for several species of fish. Besides the animals on and within the substrate, there are others attached to the plants and there are associated free-swimming organisms.

Although there is some diversity of habitat in the weed zone, certain faunal elements are characteristic (see Section IV(*a*)).

(*c*) *The Slope Zone*

At a depth of 3–4 m the large plants cease abruptly, except in some places where a sparse growth of *Halophila* reaches the mud zone at 7 or 8 m.

The substrate of the slope ranges from finer particles of sand to the pure silt of the mud zone. There is some overlap of species common to the weed zone, but characteristically the slope zone has no browsing species; instead filter feeders are dominant and a small group of carnivores occurs.

Table 1

THE HABITAT AND TYPE OF FEEDING OF THE MORE ABUNDANT MACROFAUNA OF THE WEED ZONE

Species	Habitat	Type of Feeding
Crustacea		
Actumnus tomentosus Dana	among *Zostera*	scavenger–carnivore
Chasmagnathus laevis Dana	among *Zostera*	scavenger–carnivore
Halicarcinus ovatus Stimpson	among *Zostera*	scavenger–carnivore
Leucosides leslii (Haswell)	among *Zostera*	scavenger–carnivore
Nectocarcinus integrifons (Latreille)	algal areas	scavenger–carnivore
Macrobrachium novae-hollandiae (de Man)	*Zostera* and algae	grazing–scavenger
Macrobrachium intermedius (Haswell)	*Zostera* and algae	grazing–scavenger
Metapenaeus mastersi Haswell	*Zostera* and algae	grazing–scavenger
Penaeus plebeius Hess	*Zostera* and algae	grazing–scavenger
Balanus amphitrite Darwin	solid substrate	plankton filter feeder
Cymadusa setosa (Haswell)	*Zostera* algae	scavenger filter feeder
Corophium minor Thomson	tube-dwelling on weed and stones	filter feeder
Mollusca		
Anadara trapezia (Deshayes)	on sand	plankton filter feeder
Crassostrea commercialis (Iredale & Roughley)	rocks	filter feeder
Modiolus aureolatus (Gould)	bay heads on south shores	filter feeder
Macoma tristis (Deshayes)	burrows in sand	detritus feeder
Tapes turgida Lamarck	firm sand	plankton filter feeder
Bedera hanleyi (Angas)	oyster beds	carnivore
Paracanassa ellana Iredale	weed areas	carnivore–scavenger
Pyrazus ebeninus Bruguiere	mud-sand on sheltered shores	grazer
Velacumantis australis (Quoy & Gaimard)	*Zostera*	grazer
Salinator fragilis Lamarck	sand	?

(*d*) *The Mud Zone*

A soft silt of jelly-like consistency forms the substrate of the mud zone. The surface film has a greasy look similar to that of a diatom film; but microscopic examination shows it to be due to an accumulation of faecal pellets. The water is so turbid at 7 m that there is practically no visibility. There are no plants other than a very few diatoms in the surface film. The zone is a repository of carcasses and debris from the higher zone, and scavengers are common.

IV. CHARACTERISTIC FAUNAS

(*a*) *The Weed Zone*

A great number of species occupies the diverse habitat of the weed zone; only the more common and characteristic are mentioned here.

Besides the species listed in Table 1, the Polychaeta are extremely numerous. A small capitellid species is almost invariably found in the substrate underneath *Zostera* plants.

TABLE 2

FEEDING TYPE OF THE DOMINANT ANIMALS OF THE SLOPE ZONE

Species	Feeding Type
Crustacea	
Neptunus pelagicus Linnaeus	carnivore–scavenger
Mollusca	
Octopus cyaneus Gray	carnivore
Trichomya hirsuta (Lamarck)	filter feeder
Anomia descripta Iredale	filter feeder
Venerupis crenata Lamarck	filter feeder
Chama fibula Reeve	filter feeder
Ostrea angasi Sowerby	filter feeder
Notocorbula vicaria Iredale	filter feeder
Polychaeta	
Chaetopteris varaeopedatus Renier	filter feeder
Ammochares fusiformis (Dell Chiaje)	detrital feeder
Australonereis ehlersi Hartman	filter feeder
Porifera	
Tetilla dactyloidea Carter	filter feeder
Tunicata	
Styela plicata Lesueur	filter feeder

The four crabs *Actumnus tomentosus*, *Chasmagnathus laevis*, *Halicarcinus ovatus*, and *Leucosides leslii*, are widely distributed amongst the *Zostera*. *Nectocarcinus integrifrons* is a larger crab which probably wanders into this zone. The soldier crab, *Mictyris longicarpus* Latreille, is found near the entrance channel but occurs in quantity only in Black Ned's Bay, a lagoon emptying midway down the channel.

The oyster *Crassostrea commercialis* is found attached to specimens of the snail *Velacumantis australis* as well as to rocks. The mussel *Mytilus planulatus* (Lamarck) extends well below the weed zone in other estuaries but in Lake Macquarie it has been found only on buoys floating near the surface. *Macoma tristis* is abundant in the firm sand of the weed zone, but is also found in some backwaters in soft ooze with a high organic content. The borer *Bedera hanleyi* was found in fewer numbers than the herbivorous gastropods.

The brown sea slug, *Dendrodoris gunnamatta* Allen, is occasionally found crawling on *Zostera* fronds.

(*b*) *The Slope Zone*

This zone is dominated by filter feeders, though carnivores and scavengers are present (see Table 2).

Trichomya hirsuta, *Ostrea angasi*, and *Tetilla dactyloidea* are especially typical of the slope zone, though occasionally young specimens are found in both weed and mud zones. *Octopus cyaneus* ranges into the other zones but the nests of this species, usually burrows lined and surrounded by mollusc shells, are found in the slope zone. The presence of *Octopus cyaneus* in the lake may be taken as indicative of the high chlorinities which prevail there. After a period of heavy rain several dead specimens drifted ashore.

TABLE 3

FEEDING TYPES OF DOMINANT ANIMALS OF THE MUD ZONE

Species	Feeding Type
Polychaeta	
Maldane sarsi Malmgren	iliophagous
Mesochaetopterus minuta Potts	filter feeder
Leanira japonica McIntosh	carnivorous
Lumbrinereis sphaerocephala McIntosh	carnivorous
Ophiuroidea	
Amphioplus lobatus Ljungman	scavenger–carnivore

The mussel *Trichomya hirsuta* lies in thickly packed beds which provide a distinct habitat for other animals. In estuaries to the south of Lake Macquarie the mussel *Mytilus planulatus* is dominant in the zone occupied here by *Trichomya*. A possible factor in the successful colonization of Lake Macquarie by *Trichomya* is discussed in Appendix I.

Anomia descripta, *Venerupis crenata*, and *Chama fibula* are found associated with the mussel clumps. *Anomia* is also found in numbers in the weed zone, attached to rocks and jetty piles. The small bivalve *Notocorbula vicaria* displays a range of forms which includes those described by Iredale (1930) as *N. vicaria* and *N. stolata*.

In the young stages *Tetilla dactyloidea* is fleshy, with a single exhalant aperture, and processes which anchor it in the mud; but it grows into free-lying meandering straps up to 4 m in length with many exhalant apertures.

The polychaet *Australonereis ehlersi* is found in a special habitat, the slope of the sand bank formed at the upper edge of the entrance channel. Food must be brought by the strong drift of tide as the sand is bare of other life.

(*c*) *The Mud Zone*

The number of benthic species recorded from this zone is small (Table 3). The dominant forms are polychaets and an ophiuroid.

An unidentified sabellid occurs in numbers that rival those of *Leanira* and *Lumbrinereis*, but it is not as common as *Maldane* which is the dominant form.

Maldane occupies thick-walled pillars of mud of its own construction, and feeds by ingestion of mud. The species is without gills, but the red-colourd blood shows two spectral bands (540 and 575 mμ) indicative of haemoglobin type pigment which could be of aid in times of oxygen scarcity.

Mesochaetopterus minuta occupies straw-like tubes which are not uncommon but are so small that they were overlooked at the start of the investigation.

TABLE 4

NUMBER OF ANIMALS AND BIOMASS AT SELECTED STATIONS IN THE WEED ZONE

Weed Stations		K26	L22	U15	U20	V29
Month (of 1956)		Oct.	Oct.	Sept.	Sept.	Dec.
No. of samples		1	5	1	1	5
Metapenaeus	Wt. (g)		22·8			
	No.		16			
Cymadusa	Wt. (g)		1·3	7·2		1·2
	No.		62	250		70
Crabs	Wt. (g)		2·8			2·4
	No.		26			28
Polychaets	Wt. (g)		6·0		11·6	6·1
	No.		194	20	132	258
Macoma	Wt. (g)		2·4	27·9	114·1	16·2
	No.		108	20	14	26
Laternula	Wt. (g)		23·1			2·0
	No.		28			12
Cavitidens	Wt. (g)					4·8
	No.					6
Paracanassa	Wt. (g)		14·4	31·1	6·4	4·2
	No.		174	250	24	42
Velacumantis	Wt. (g)	129·9	0·9	546·0	102·3	19·9
	No.	41	8	190	60	60
Anadara	Wt. (g)			15·5		3·9
	No.			20		16
Trichomya	Wt. (g)					12·7
	No.					8
Miscellaneous molluscs	Wt. (g)		4·1			4·0
	No.		12			8

The ophiuroid *Amphioplus lobatus* is a small species found throughout the mud zone but in greatest concentrations in the neighbourhood of Coal Point, where *Maldane* happens to be scarce. The normal habit of this species seems to be to lie with the disk submerged and the arms reaching above the mud surface.

Two molluscs, *Myadora brevis* (Stuchbury) and *Cardium racketti* Donovan, have been taken in the mud zone in small numbers. Other molluscs whose dead shells are common in the mud are *Notovola fumata* Reeve, *Paratapes scordalus* Iredale, *Notospisula cretacea* Angas, *Dosinia sculpta* Hanley, and *Cavitidens omissa*

Iredale. The shells are usually found articulated and well preserved and only in the later stages of the investigation were young live specimens of *Notospisula* and one live specimen of *Paratapes* found.

The scallop *Notovola fumata* is stated by local residents to have been abundant within living memory, but no live specimens were collected during this study.

TABLE 5

NUMBER OF ANIMALS AND BIOMASS AT SELECTED STATIONS IN THE SLOPE ZONE

Slope Stations		S22	T16	T17	U14
Month (of 1956)		Sept.	Nov.	Sept.	Sept.
No. of samples		4	1	2	5
C. varaeopedatus tubes	No.	20			
Ammochares	Wt. (g)				
	No.	25	630		34
Australonereis	Wt. (g)			172·6	
	No.			1750	
Other worms	Wt. (g)				
	No.	43	10	30	32
Notocorbula	Wt. (g)				
	No.	10			
Notospisula	Wt. (g)			7·8	
	No.			135	4
Other molluscs	Wt. (g)				
	No.	3		10	
Crustaceans	Wt. (g)				
	No.	3		15	

V. QUANTITATIVE ESTIMATES

(*a*) *The Weed Zone*

The density of several species at typical stations in the weed zone is shown in Table 4. It is evident that both the composition and the density of the fauna are extremely variable between stations. Excluding one station at which unusually high densities occurred, a mean figure derived for the fauna of the weed zone is 94 ± 56 g/m^2.

(*b*) *The Slope Zone*

The variation in composition and density between samples is great in this zone also. Difficulties were encountered in sampling adequately the infauna and the large clumps of *Tetilla dactyloidea* and of *Trichomya hirsuta*. Because of the mechanical difficulties of measuring these, figures quoted in Table 5 refer only to an area on the east side of the lake from Galgabba to Belmont Bay where the substrate is of firm sand. *Tetilla* and *Trichomya* are absent and the dominant forms are polychaets, particularly *Australonereis ehlersi*. The biomass in this area is 180 ± 12 g/m^2.

TABLE 6

NUMBER OF ANIMALS AND BIOMASS AT SELECTED STATIONS IN THE MUD ZONE

Mud Stations		O9	O9	O23	P29	Q13	Q13
Date		May 56	Sept. 56	Oct. 56	Oct. 56	Sept. 56	Dec. 56
No. of samples		4	5	5	5	5	5
Maldane	Wt. (g)	4·3	4·6	1·4		5·1	8·1
	No.	303	76	324		162	414
Other worms	Wt. (g)		2·1	1·3	1·1	1·3	10·8
	No.	15	58	32	32	22	302
Amphioplus	Wt. (g)						0·7
	No.	3	2		2		12
Crustaceans	Wt. (g)						1·4
	No.	5	2	8	4		12
Molluscs	Wt. (g)		1·0	0·2	1·2		0·3
	No.	10	18	4	6	2	8

Mud Stations		Q13	Q25	R16	R16	R32	R32
Date		Jan. 57	Nov. 56	July 56	Dec. 56	Nov. 56	Feb. 57
No. of samples		5	5	5	5	5	4
Maldane	Wt. (g)	6·6	0·6	1·1	0·6	27·7	9·7
	No.	402	102	16	120	256	62
Other worms	Wt. (g)	1·7	0·4	2·9	4·0	0·2	0·8
	No.	150	6	78	174	16	28
Amphioplus	Wt. (g)			16·2	22·8		
	No.	10		146	172		
Crustaceans	Wt. (g)		0·1		0·7	0·7	1·1
	No.		4	2	4	30	73
Molluscs	Wt. (g)	0·7	0·3			0·2	15·6*
	No.	6	8			6	3

Mud Stations		S15	T21	T21	T22	U27	U27	U27
Date		May 56	July 56	Jan. 56	Sept. 56	Nov. 56	Dec. 56	Feb. 56
No. of samples		3	5	5	5	5	5	5
Maldane	Wt. (g)		5·6	0·6	0·3	0·8	5·4	16·4
	No.	167	172	34	10	184	552	910
Other worms	Wt. (g)		2·0	5·5	0·4		1·8	1·5
	No.	43	124	52	16		20	102
Amphioplus	Wt. (g)		0·3	25·0				
	No.	340	6	216				
Crustaceans	Wt. (g)				0·8	0·1		
	No.	7			2	2		2
Molluscs	Wt. (g)				2·2	0·7	0·2	0·2
	No.	17			4	12	2	6

* Large shell.

(c) *The Mud Zone*

Although in qualitative sampling the mud fauna appeared homogeneous with a single dominant species, the quantitative sampling showed distribution to be patchy (Table 6), the biomass being 10·6±9·4 g/m².

The ophiuroid *Amphioplus* was found scattered throughout the mud zone, but near the entrance channel the population was so dense that the animals overlapped.

TABLE 7

VARIABILITY IN BIOMASS AS BETWEEN STATIONS AND BETWEEN SAMPLES FROM ONE STATION

Station	Date	Zone	Weights (g/m²)					Totals	Means
K26	Oct. 56	weed	129·9					129·9	129·9
L22	Oct. 56	weed	105·2	106·1	82·1	53·1	62·2	409·2	81·8
O9	Sept. 56	mud	7·6	11·6	5·6	11·0	3·0	38·8	7·8
O23	Oct. 56	mud	1·6	3·9	3·6	2·9	2·4	14·4	2·9
P29	Oct. 56	mud	2·0	0·2	1·9	0·6	6·9	11·6	2·3
Q13	Sept. 56	mud	6·6	5·5	2·5	7·3	10·0	31·9	6·4
Q13	Dec. 56	mud	3·6	66·9	13·1	14·6	7·9	106·1	21·2
Q13	Jan. 57	mud	16·9	5·2	5·3	5·5	12·1	45·0	9·0
Q25	Nov. 56	mud	3·7	—	2·4	0·6	0·2	6·9	1·4
R16	July 56	mud	15·4	10·7	25·7	23·7	24·0	103·1	20·6
R16	Dec. 56	mud	25·0	17·0	21·9	33·3	43·5	140·7	28·1
R32	Nov. 56	mud	20·8	28·6	10·5	33·8	50·2	143·9	28·8
R32	Feb. 57	mud	67·6	19·5	18·0	3·7	—	108·6	27·2
T17	Sept. 56	slope	193·1	168·9				362·0	181·0
T21	July 56	mud	6·5	6·6	7·8	7·4	11·1	39·4	7·9
T21	Jan. 57	mud	42·7	39·1	35·2	12·8	15·6	145·4	29·1
T22	Sept. 56	mud	3·7	11·9	2·0	0·5	—	18·1	3·6
U15	Sept. 56	weed	627·7					627·7	627·7
U20	Sept. 56	weed	234·4					234·4	234·4
U27	Nov. 56	mud	1·7	2·4	1·9	0·6	1·2	7·8	1·6
U27	Dec. 56	mud	4·6	8·1	10·1	7·6	6·7	37·1	7·4
U27	Feb. 57	mud	21·2	15·2	9·2	23·2	21·6	90·4	18·1
V29	Dec. 56	weed	85·5	62·0	29·6	110·6	102·2	389·9	78·0

(d) *Relative Contribution of the Zones*

Despite the variable densities of any one zone, Table 7 shows clearly that the relatively smaller areas of the weed and slope zones have faunal densities considerably higher than that of the mud zone and, in fact, must make a much higher contribution to the total bottom fauna.

Where *Tetilla* and *Trichomya* dominate in the muddier areas, distribution is patchy, but the density within the patches is such that the yield per m² remains high. The higher zones, particularly the weed zone, include several heavy-shelled molluscs whose life span is prolonged, whereas observations on the mud fauna suggest that there is an annual replacement of worms. Even so, the annual production of the weed and slope zone exceeds that of the mud.

The biomass values for some overseas areas studied (F.A.O. Biology Branch, Fisheries Division 1956) are: Italian coast 6 g/m², Bay of Algiers 18·7 g/m², and North Atlantic and North Sea areas from 200 to 300 g/m². The mud zone of Lake Macquarie thus produces about the same as the poor grounds of the Mediterranean, and the slope zone almost reaches densities typical of the North Atlantic.

VI. Biological Non-Homogeneity of the Benthos

Although to casual observation the habitat occupied by a particular species appeared to be uniform, differences in growth rate, spawning time, and size distribution of the populations were found when samples were taken from different parts of the lake.

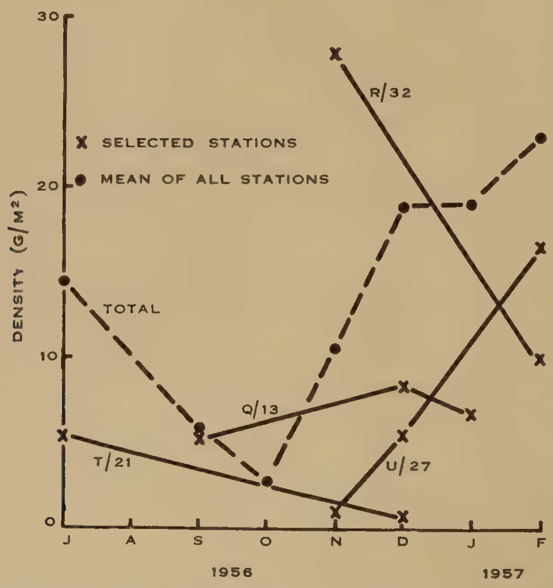

Fig. 1.—Seasonal variation in biomass of all species of the mud zone.

The polychaet, *Maldane sarsi*, occupies the mud zone of the lake. In Figure 1 a seasonal curve of biomass based on the means for all stations shows a seasonal decline, which qualitatively results from the disappearance of most large *Maldane* after the spring spawning. The young worms appear in September and October and grow rapidly from a length of 1·5 cm, when they are first retained by the sieves, to a size of 2–4 cm in February. However, examination of individual stations revealed marked differences. This is apparent in Figure 1 where the curves for four stations are given. Extreme differences are shown by Stations R32 and U27. In the former case, large worms with eggs persisted without appearance of young worms and the population declined in biomass owing to mortality. At U27 a population of small worms showed steady growth. The average weights per worm shown in Figure 2 illustrate the difference in the stage of development of worms at various stations.

Similar lack of homogeneity within the total population was shown by the molluscs *Anadara trapezia* and *Velacumantis australis*. The heavy-shelled *Anadara* is widely distributed in the weed zone, sometimes occurring in dense patches. In September 1955 two local samples, one from Pt. Wolstoncroft and the other from Marmong Pt., were measured. The hinge lengths were 2·0±0·2 cm and 3·6±0·2 cm respectively. This would seem to indicate either that the two samples were of different age and thus of settling time, or that different rates of growth prevail in different parts of the lake.

Samples of *Velacumantis* showed great difference in size distribution from place to place. Probably closer examination would show similar differences between local populations of other species. However, these three widespread species indicate that biologically the lake does not function as a unit.

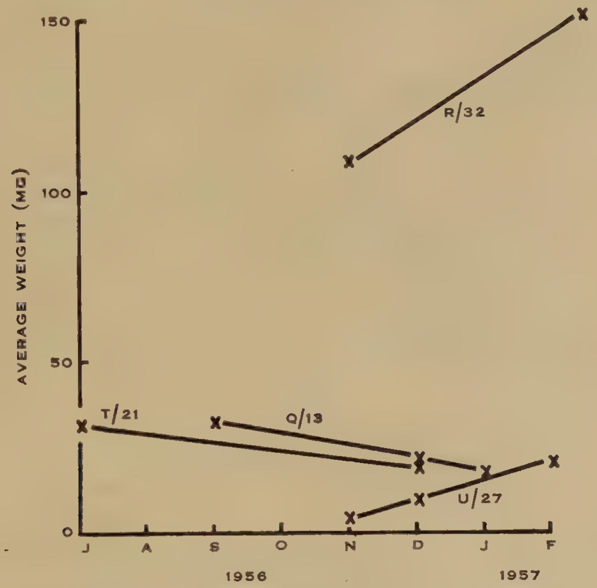

Fig. 2.—Seasonal variation in average weight per worm at selected stations.

VII. Acknowledgments

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APPENDIX I

THE SPAWNING AND RESISTANCE TO ANAEROBIC CONDITIONS OF TRICHOMYA HIRSUTA

(a) *Spawning Time*

The mussel *Trichomya hirsuta* is a very abundant organism in the slope zone. When it was studied for evidence of the non-homogeneity displayed by certain other abundant animals (Section V), it was found that not only did samples from various areas show similar size distributions but also that even up to a size of 7 cm the graph of size distributions showed no modes that could be interpreted as representing year (or size) groups. Yet some experimental work suggested that growth is slow. A wire cage containing 50 mussels was suspended 50 cm above a mud bottom and a similar cage of 50 mussels above a sandy bottom in depths of 10 and 5 m respectively.

The mean growth of mussels was, from June to December: sand 0·05 cm, mud 0·04 cm; from December to June: sand 0·21 cm, mud 0·23 cm.

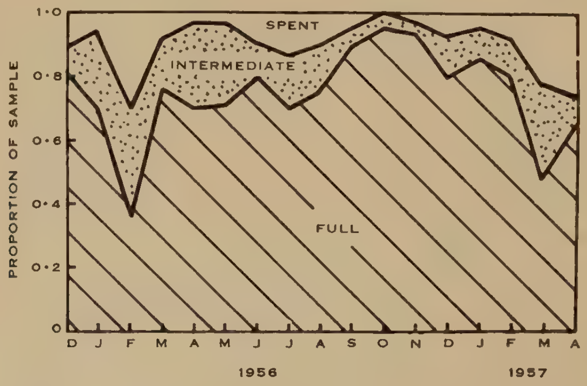

Fig. 3.—Seasonal gonad condition of *Trichomya hirsuta*.

This may be less than the normal growth, owing to the abnormal situation; but if this rate of growth is accepted, it would suggest that the larger shells reach 7 years of age.

The graph of size-distribution of the mussels showed an immense preponderance of juveniles up to 0·5 cm and this was a persistent condition at all times of the year. This suggested that spawning and settlement proceeded throughout the year and that there was a large mortality. Monthly samples of 40–50 gonads (Fig. 3) supported this hypothesis as active sperm and ova were present throughout the year.

(b) *Resistance to Anaerobic Conditions*

Mention was made in Section IV of the fact that in Lake Macquarie *Trichomya* replaces *Mytilus planulatus*, which is abundant in the slope zone of estuaries to the south.

That some sort of catastrophe may have occurred in the lake fauna is suggested by the presence of well-preserved dead shells of certain molluscs, including

Notovola fumata, *Paratapes scordalus*, *Notospisula cretacea*, *Dosonia sculpta*, and *Cavitidens omissa* in the mud zone although no live specimens were found. One hypothesis is that a temporary anaerobic condition of the bottom of the lake may have been responsible.

Some laboratory experiments were performed to compare the resistance of *Trichomya hirsuta* and that of its ecological counterpart *Mytilus planulatus* to anaerobic conditions. Specimens collected from one area of Port Jackson were acclimatized in aquarium tanks prior to being confined in separate sealed jars of deoxygenated sea-water under a layer of paraffin oil. The initial E_h was below —100 mV.

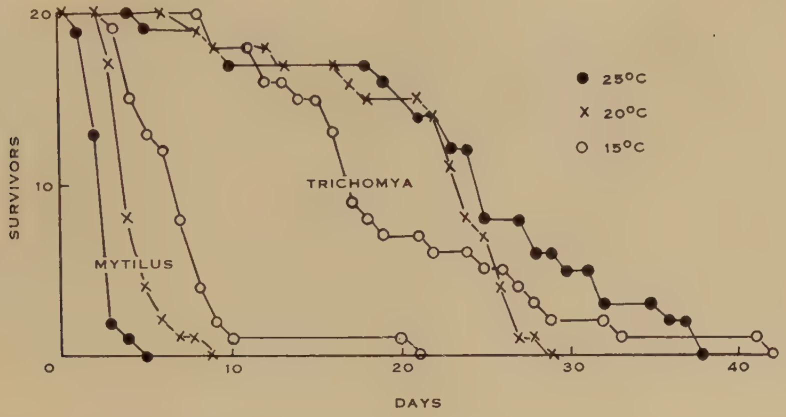

Fig. 4.—Survival time of *Mytilus planulatus* and *Trichomya hirsuta* in deoxygenated water at various temperatures.

In a preliminary experiment at 26°C with 20 pairs, *Mytilus* died in 4 days whereas *Trichomya* survived 32 days. As this temperature could well be near the upper limit of tolerance of *Mytilus* the experiment was repeated with lower temperatures, with the result shown in Figure 4. At all three temperatures tested, *Trichomya* showed significantly greater powers of survival.

SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

VIII. TRENDS OF THE COMMERCIAL FISH CATCH AND MANAGEMENT OF THE FISHERY

By J. M. Thomson*

[*Manuscript received February 5, 1959*]

Summary

Although the total catch has fallen since 1922 the abundance of fish as measured by the catch per man has not. The total catch has dropped because fewer men are fishing. A real drop in the abundance of certain species, namely flathead, bream, luderick, and sea mullet, occurred between 1945 and 1947; the algal-feeding luderick and mullet regained their abundance by 1951, but the three ground fish had not regained their former abundance by 1957.

The trends of the monthly catch are similar in all years, the catch expectation being least reliable in November and most predictable in February.

Closing of the northern end of the lake to commercial fishing has resulted in a loss to the consumer of quantities of sea mullet and tailor, species which are fished ineffectively by amateur anglers. During the winter months netting in the northern part of the lake, except in certain bays which form nursery grounds for the young of several species, would have no injurious effect on the stocks.

I. Trends of Annual Catch

The trends of catch are shown in Figure 1. Since 1922 the catch has fallen. From 1913 to 1936 the catch per man was lower than in the preceding 20 years, but from 1938 it increased again. There has been no change in the type of gear used (mesh nets and hauling nets) over the years, except that now some fishermen use nylon instead of linen. Fishing habits remain the same; generally fishing operations are confined to 4 or 5 days per week, consisting of one overnight set of mesh nets, or one major haul of the hauling nets per day. The only statistics collected by the administering authority in New South Wales are the monthly and annual catch figures and the number of men. A more precise measure of effort than the number of men is lacking, so that, despite the defects of this parameter, it has been utilized as a measure of the intensity of fishing.

The drop in the total catch and of the catch per man during the period 1922–38 is not interpreted as a sign of depletion. It is thought that the total catch fell because fewer men fished, not because fish became less abundant; and that the catch per man fell because over this period there was less inducement to fish because of poor prices received. Subsequent to 1922 the estuarine fishing industry was faced with competition for the fresh fish market from the rapidly growing trawler industry. Marketing and distribution arrangements were such that the increased catch potential could not be fully absorbed (see the Annual Reports of

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the New South Wales Department of Fisheries for 1925, 1926, 1927, 1928, and 1929). These reports make it clear that, in contemporary opinion, the fall in estuarine catch was due to lack of economic incentive to fish and that estuarine fish stocks were in good condition. Thomson (1953) has discussed the effects both of the trawling industry and of imported fish products on the estuarine fisheries. Conditions presumably affected equally Lake Macquarie and other coastal areas.

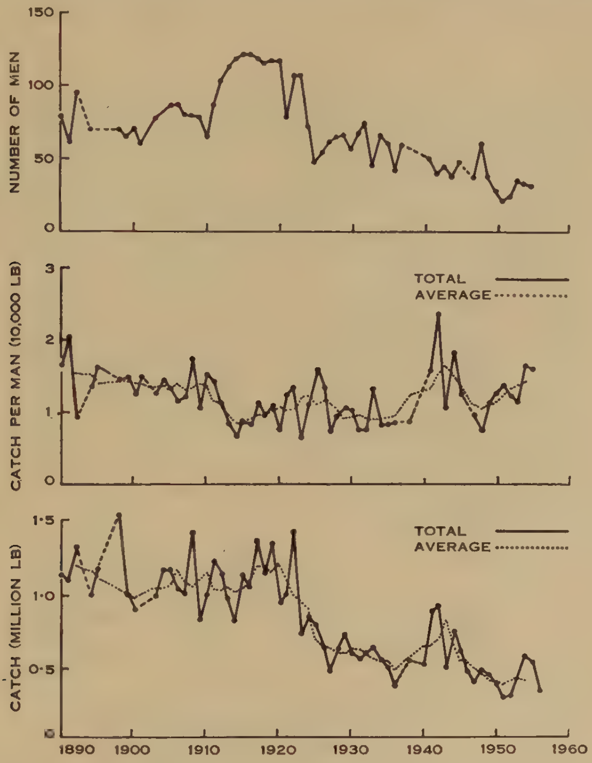

Fig. 1.—The total catch, catch per man, and number of men, Lake Macquarie, 1890–1956.

When economic incentive returned, as during the war years, estuarine catches rose and the catch per man increased. With the immediate post-war influx of inexperienced fishermen into the industry the catch per man was lowered, to increase again as the least efficient left in the industry. In 1948 there was applied for the first time a State law restricting the issue of fishing licences to those who would work as full-time fishermen. The number of men shown in Figure 1 is not the total of licences issued for the district but the annual arithmetic mean number, weighted by months, of those actually marketing fish.

The effect, first of trawling and later of management policies, has been to reduce the number of fishermen suddenly at two periods. The three phases of the fishery are distinguishable in Figure 2.

II. Composition of the Catch

The proportion of the more important species in the Lake Macquarie catch over the years 1940–41 to 1955–56 is indicated in Figure 3. Sea mullet, *Mugil cephalus* L., has been the dominant species, varying from 24 per cent. in 1945 to 72·5 per cent. in 1954. In certain years, particularly from 1945 to 1949 and again in 1952, leatherjackets were plentiful, but after 1953 they became relatively unimportant. Tailor, luderick, and bream have been fairly well represented in the catch. Other species which at least in some years have provided an important portion of the catch are dusky flathead, river garfish, tarwhine, mulloway, snapper, and salmon. Other species which made only a small contribution to the catch included sea garfish, yellowtail, trevally, flat-tail and telegalene mullets, teraglin, morwong, and flake. Prawns and crabs are also marketed from the lake (Fig. 4). Crayfish are sometimes recorded as being caught in Lake Macquarie but actually they are caught from the headlands and islands outside the entrance to the lake and do not form part of the lake fauna.

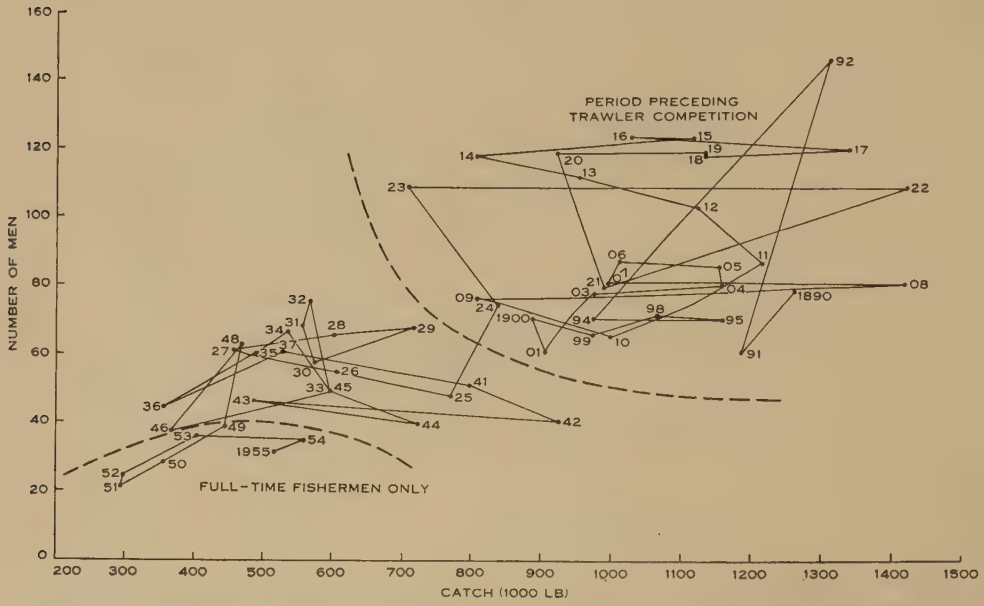

Fig. 2.—Relationship of catch to number of men; indicating three phases in the fishery: 1890–1924; 1925–48; 1949–56.

Data published prior to 1954 in the State Fisheries Annual Reports include catches from the inshore area immediately outside the lake. Since 1954 the catch from this area has been tabulated separately but the figures indicate that its contribution to the total is slight except in the case of leatherjackets, of whose number over half was fished from outside the lake in 1954 and about 45 per cent. in 1955. It would seem therefore that the figures for leatherjackets should be interpreted with caution, but the trends for other species probably reflect events within the lake.

The trends of the annual catch of the more important species for the years 1941 to 1956 are shown in Figure 5. The catch per man for the same period is illustrated in Figure 6. It is true that the efficiency of the fishing might vary from year to year and as mentioned above this is almost certainly the case in 1948 and it can be seen that this was a year of low catch per man for all species except snapper and tailor.

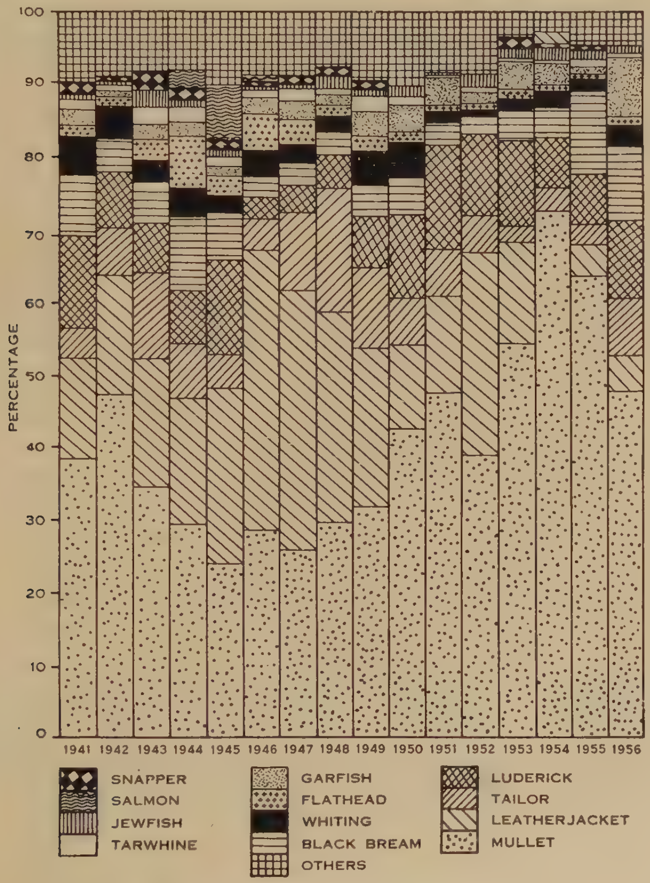

Fig. 3.—Catch composition, Lake Macquarie, 1941–56.

It is evident from Figure 6 that a real drop in the abundance of several species, namely flathead, bream, whiting, luderick, and sea mullet occurred between 1945 and 1947, and that the time of recovery varied with the species, and indeed, apart from bream in 1955, the three ground fish did not afterwards regain their former abundance. The algal-feeding luderick and mullet had recovered their abundance by 1951.

III. Trends of Monthly Catch

Monthly catch data for each species are available only for two years, 1954–55 and 1955–56, and these show variable catches. However, figures are available in the Department of Fisheries' Annual Reports for a series of eight years for all species. These show (Table 1) that over the period considered the year-to-year variation in total catch per man in any particular month was not very great. November is the month in which greatest variability of catch occurred (coefficient of variation 61 per cent.). February is the month with least variation (coefficient of variation 19 per cent.). The catch of mullet was more variable than the catch of all other species combined, but the smaller variability in this latter group may be fortuitous as a result of the many environmental factors acting on the various species of fish to produce fluctuations that, in a statistical sense, are random and more or less cancel out one another.

Table 1

MEAN CATCH PER MAN IN EACH MONTH FOR THE PERIOD FROM THE YEAR ENDING JUNE 1948 TO THE YEAR ENDING JUNE 1955, WITH THE COEFFICIENT OF VARIATION

Month	Mullet		Other Species		All Species	
	Mean Catch (lb)	Coeff. of Variation	Mean Catch (lb)	Coeff. of Variation	Mean Catch (lb)	Coeff. of Variation
July	249	75·1	421	33·5	670	31·2
August	245	91·4	474	48·3	719	41·9
September	337	85·7	560	37·8	897	43·6
October	505	80·2	708	25·7	1213	48·1
November	566	89·2	601	32·3	1167	61·1
December	710	43·4	441	27·4	1151	29·9
January	959	42·0	499	31·7	1458	24·2
February	544	44·8	575	49·0	1119	19·1
March	574	70·4	539	34·9	1113	32·9
April	735	40·7	587	36·8	1322	23·4
May	486	63·8	771	28·9	1257	23·8
June	420	65·2	609	26·6	1029	33·2

IV. Fisheries Management

(*a*) *Control of Nets and Closed Waters*

The records of the Fisheries Department were destroyed by fire in 1882 and the managerial policies enforced prior to that date are not known. It would appear from the report of the Fisheries Enquiry Commission in 1880 that regulations probably did not exist, or at least were not enforced, for reference is made in the report to an Act in existence whose provisions were moribund. Oliver (1893) refers to the Fisheries Act, 1881, as being "without doubt the first formal attempt at comprehensive legislation based on the principle of protecting the natural supplies of fish and of regulating and controlling their capture".

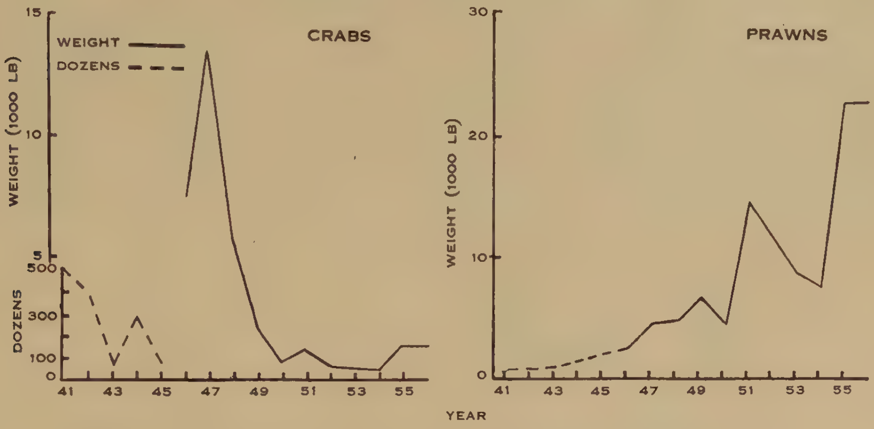

Fig. 4.—Commercial catch of prawns and crabs, Lake Macquarie, 1941–56.

The Fisheries Act, 1881, and the regulations made in its administration, included general provisions about dimensions of nets which applied equally to Lake Macquarie as to other waters of New South Wales. The first managerial regulation applying particularly to Lake Macquarie appears to have been a regulation issued

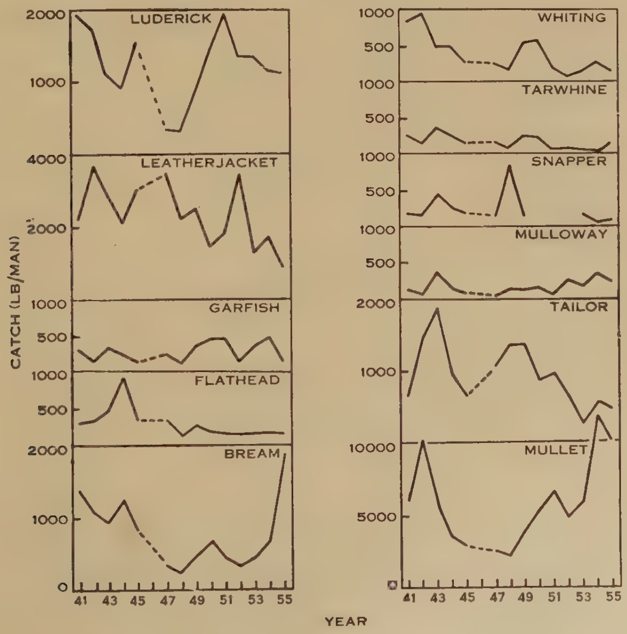

Fig. 5.—Catch curves of eleven commercial species, Lake Macquarie, 1941–56.

in 1883 (according to the Report of the New South Wales Fisheries Commissioners for 1884), which closed the entrance waters to fishing by nets. Except for a few brief intervals of a few weeks the entrance waters have remained closed to net fishing ever since. The tributaries were closed to net fishing in 1886, according to the Fisheries Commissioners' report for 1887.

It is not clear whether the regulation closing the entrance channels also included portion of the main lake. In the Fisheries Commissioners' report for 1897, Belmont Bay was mentioned as part of the waters fished when the closed waters were open for 30 days in 1895. When the closed waters were precisely defined in 1903 they did not include Belmont Bay, but did include Swan Bay and part of Swansea flats (see Fig. 7, hatched area). Subsequently, except for a few weeks in 1906 and 1909, this area has remained closed to the use of all nets other than the prescribed dip or scoop net for taking prawns, except that garfish nets were permitted for 3 months in 1928.

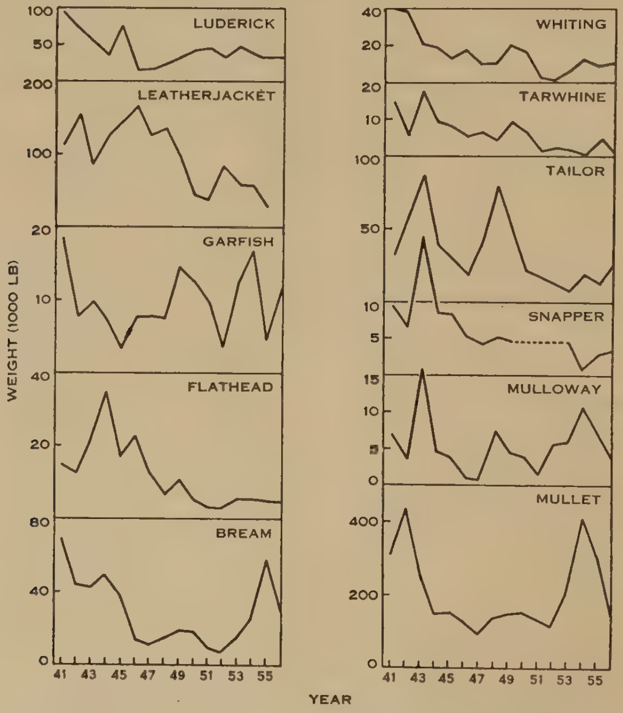

Fig. 6.—Catch per man of eleven commercial species, Lake Macquarie, 1941–56.

Since 1906 there has been more or less constant agitation on behalf of angling and tourist interest to have some or all of the lake closed to netting in order to preserve the fishing for line fishing (see the Report of the New South Wales Fisheries Commissioners for 1907 and subsequent reports).

The waters of Toronto Bay were closed to net fishermen for 9 months from June 1, 1916.

For 12 months from February 17, 1930, the waters of Kilaben and Erraring Bays were closed to netting (Fig. 7, lines 1, 2). From February 10, 1933, to November 15, 1936, netting was prohibited in Belmont and Village Bays (Fig. 7, lines 2, 3). Since 1936 the whole of Lake Macquarie north of a line between Wangi Point and Galgabba Point (Fig. 7, line 4) has been closed to netting other than by prescribed prawn nets except for 2 months in autumn in 1943 and 1944, and for the winter months (May to October) in 1956 and 1957, when mesh nets were permitted.

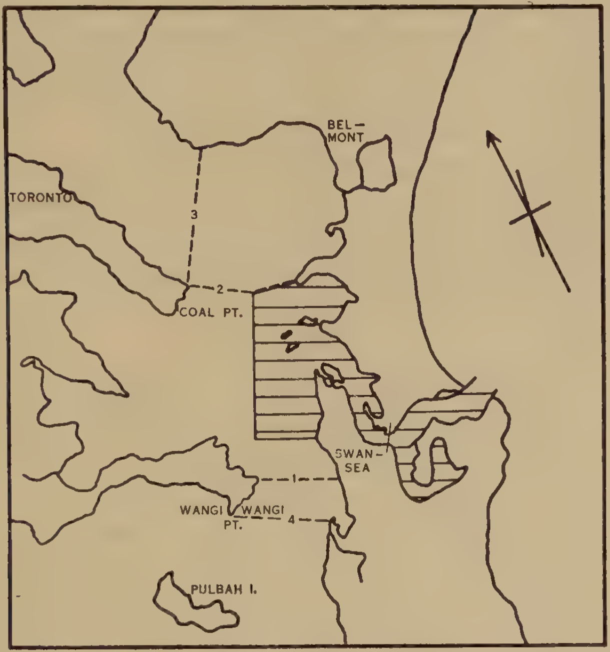

Fig. 7.—The closed waters of Lake Macquarie. "Entrance waters" hatched. Closed February 1930 to February 1931 between lines 1 and 2. Closed February 1933 to November 1936 between lines 2 and 3. All waters north of line 4 closed 1936 to date except for relaxation of mesh netting May 1956 to September 1957 excluding two bays.

(*b*) *Control of Lines and Traps*

The use of long-lines in the entrance channel was forbidden for 3 years from July 29, 1915. They have been prohibited since March 1928. Use of long-lines was prohibited in Belmont and Village Bays from February 10, 1933 to November 15, 1936; and they have been banned in the whole lake since November 1936.

The use of traps has been forbidden in the entrance channel since March 1931; in Belmont and Village Bays since February 1933; and in the whole lake since November 1936.

Snares for the capture of crabs have been prohibited since July 1940.

(c) *Control of Environment*

The channel was dredged for many years. Although this was primarily to facilitate passage of small ships it was believed by many connected with the fishing industry that the enhanced tidal flow brought about would attract more fish into the lake. At the same time the continual dredging removed food and plant shelter, and prevented the re-establishment of the natural communities. The channel in itself must be regarded as an improved environment for fish since dredging ceased, as it has been repopulated except for the purely sandy bottom at the sea and lake ends. The depth to which the channel was dredged could have had an effect on the substrate of the lake and thus on the benthic food organisms, but charts (Baas Becking, Thomson, and Wood 1959) do not show any appreciable alteration to the depth of the sand bar at the inner end of the channel. The improved flow of water consequent upon dredging may well have had an effect on the amount of mero- and holo-plankton entering the lake from outside, and would also permit more rapid drainage of the lake during rainy periods.

Worms and nippers (the crustaceans *Crangon edwardsii* (Audouin) and *Callianassa australiensis* (Dana)) are important food organisms for certain angling fish and are therefore much prized as bait. Digging for these so disturbed the flats that it has been prohibited since March 1943.

(d) *Effects and Observance of the Regulations*

Until interim recommendations based on the present investigations were acted upon in 1956 and 1957, no commercial fishing had been permitted in the northern part of the lake since 1936.

Tagging results (Thomson 1959) suggested that except for flat-tail mullet there was little interchange of fish between the northern and southern portions of the lake. This meant that the abundant sea mullet population of the northern part remained largely unfished prior to migration from the lake as this species does not bite readily on a hook and relatively few are taken by anglers. It may be stated, too, that it is by no means certain that angling is an effective method of catching other species. It is common experience for areas which anglers have declared to be without fish to yield a substantial catch to net fishermen.

As a result of this investigation mesh nets were permitted in the northern part of the lake during the winters of 1956 and 1957. Hauling nets which would have had to be pulled ashore on beaches which are adjacent to nursery areas of fish fry were not permitted.

Sea mullet and tailor were the species taken in greatest numbers in this period, though lesser quantities of bream, luderick, and flathead were also taken. The angling pressure in winter months is low and the species forming the bulk of the catch are exploited only slightly by anglers. Opening the northern part of the lake to mesh netting during winter months will yield fish which otherwise might well pass from the lake. Observations in the southern part of the lake suggest that the majority of commercial fishermen respect the regulations which are designed to protect their livelihood. Mesh nets are almost all of a mesh greater than the legal minimum as nets of legal size do not retain the run of large mullet.

During the course of these investigations the legal mesh size of the bunt of hauling nets was changed from 1½ in. to 2 in. After some months this regulation was amended to its original form, i.e. a bunt of 1½ in. It is the present author's opinion that increasing the mesh was detrimental to the spinous species such as bream, tarwhine, and squire, because small sizes of these fish predominated on the major hauling grounds and were meshed in the larger bunt, many dying of asphyxiation or being injured before release. In the smaller mesh bunt these size groups were retained without meshing and were released without injury. The smaller mesh does retain small mullet but these are not very abundant on the hauling grounds in Lake Macquarie, their usual habitat being in the lagoons, along shallow shores, and in creeks.

It is true that at times, even with the small mesh, quantities of small fish can be seen lying dead after hauling. Investigation on numerous occasions showed the only species killed in number was the silverbelly, *Gerres ovatus* Gunther.

One practice that needs correction is the habit of some fishermen, more particularly those operating in the south-western part of the lake, of hauling their nets right ashore instead of into a back-net, which is the usual practice amongst fishermen in the south-east of the lake. Hauls beached and sorted ashore inevitably result in loss of fish.

Because of restrictions in the type of gear permitted and in the areas which may be fished, prawn production in Lake Macquarie is small. However, the use of efficient catching gear such as otter trawls could lead to undesirable consequences as small squire are abundant in the lake and were taken in quantity in the experimental prawn trawls used during these investigations.

V. Recommended Management Measures

For reasons already discussed in the previous section, the following specific measures are recommended:

(1) The open waters of the northern part of the lake should be open to mesh netting from May to October each year.

(2) The headwaters of all bays in the northern part of the lake and the waters of all lagoons around the lake should be closed to net fishing.

(3) The channel waters, including Swan Bay and the portion of Swansea flats immediately adjacent to the entrance channel, should be closed to commercial fishing to avoid interference with the movement of migrating fish.

(4) Active steps should be taken to discourage the taking of undersized fish by anglers, as well as by professional fishermen.

(5) Prawn trawling should not be permitted in the lake.

(6) In Lake Macquarie the mesh of the bunt of hauling nets should be fixed at 2 in.

It is quite probable that, other things being equal, the situation shown in Figure 2 for the early years, namely a much higher catch and more men employed, could be regained by throwing open the whole lake to commercial exploitation. However, since the period 1890–1924, the number of anglers frequenting the lake must have risen considerably and it is doubtful if the return to the catches of this early period would be possible because of competition from the anglers. Nevertheless, an increased commercial catch should be achieved by implementation of the first recommendation listed above.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

IX. THE FISHES AND THEIR FOOD

By J. M. Thomson*

[*Manuscript received February* 5, 1959]

Summary

During this investigation, 103 species of fish were taken in Lake Macquarie. Thirty-four are fishes of commerce, though only 12 are of local importance. There are no food records of 24 species; of the others, eight are herbivores, 13 omnivores, and 58 carnivores. In the last group are 27 microphagous and 31 macrophagous species. All but six of the macrophagous species consume fish, mostly hardyheads and gobies. Relatively few commercial species of fish were found in fish stomachs. Twelve species of planktivorous fish are distinguished.

I. Introduction

Although the fish fauna of New South Wales was reported upon by McCulloch (1934), there are only fragmentary lists of the fish from one locality. Little is known about the feeding habits of most of the fish which occur in New South Wales other than the types of bait which attract the favoured angling fish. This study attempts firstly to determine what species of fish occur in the lake, and secondly to ascertain their food habits.

II. The Fish Fauna

During the course of the Lake Macquarie investigations, 103 species of fish were identified by the present author making use of this Laboratory's catalogue (Munro 1952). These fishes are listed in Table 1.

Of these fish the only new record for New South Wales is *Stenatherina honoriae*, the estuarine hardyhead, which, however, is known from southern Queensland. One species, the poecilid *Gambusia affinis* is an introduced species used for mosquito control. Some fishes recorded here are known as stragglers into New South Wales waters, but are more truly tropical species. These are:

Alectis ciliaris
Diodon holocanthus
Equulites moretonensis
Monodactylus argenteus
Ovoides aerostaticus
Stenatherina honoriae
Suggrundus jugosus
Therapon servus
Trachynocephalus myops

Some 34 of the species recorded are fishes of commerce, but only 12 are of any particular importance in the Lake Macquarie fishery (Thomson 1959).

Of the 57 families recorded only 23 contribute more than one species to the fauna, the Gobiidae with seven species and the Syngnathidae with six being the best represented.

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TABLE 1

THE SPECIES OF FISH RECORDED FROM LAKE MACQUARIE

Those marked * were taken only in Black Ned's Bay (Baas Becking, Thomson, and Wood 1959, Fig. 1) and not in the main lake

Family	Species	Common Name
Heterodontidae	*Heterodontus portusjacksoni* (Meyer)	Port Jackson shark
Dasyatidae	*Urolophus testaceus* (Müller & Henle)	Common stingray
Clypeidae	*Sardinops neopilchardus* (Steindachner)	Pilchard
	Harengula abbreviata (Valenciennes)	Southern herring
	Hyperlophus vittatus (Castelnau)	Sandy sprat
Engraulidae	*Engraulis australis* White	Anchovy
Galaxiidae	*Galaxias attenuatus* (Jenyns)	Jollytail
Anguillidae	*Anguilla australis* Richardson	Short-finned eel
Echelidae	*Muraenichthys australis* Macleay	Worm eel
Ophichthyidae	*Ophisurus serpens* (Linnaeus)	Snake eel
Plotosidae	*Plotosus anguillarus* (Bloch)	Striped catfish
	Cnidoglanis macrocephalus (Valenciennes)	Estuary catfish
Synodontidae	*Trachynocephalus myops* (Bloch & Schneider)	Painted saury
Poecelidae	*Gambusia affinis* (Girard)	Mosquito fish
Belonidae	*Tylosurus macleayanus* (Ogilby)	Stout long tom
Hemirhamphidae	*Hemirhamphus ardelio* (Whitley)	River garfish
	Hemirhamphus australis Steindachner	Sea garfish
Bothidae	*Pseudorhombus jenynsii* Bleeker	Small-toothed flounder
Soleidae	*Aseraggodes macleayanus* (Ramsay)*	Narrow-banded sole
	Achlyopa nigra Macleay	Black sole
Zeidae	*Zeus faber* Linnaeus	John dory
Berycidae	*Centroberyx affinis* (Gunther)	Nannygai
Syngnathidae	*Yozia tigris* (Castelnau)	Tiger pipefish
	Urocampus carinirostris Castelnau	Snub-nose pipefish
	Stigmatopora argus (Richardson)	Spotted seahorse
	Stigmatopora nigra Kaup	Broad pipefish
	Syngnathus margaritifer (Peters)	Angular pipefish
	Hippocampus whitei Bleeker	Australian seahorse
Fistulariidae	*Fistularia petimba* Lacepède	Flute-mouth
Atherinidae	*Taeniomembras microstomus* (Gunther)	Small-mouthed hardyhead
	Pranesus ogilbyi Whitley	Eastern hardyhead
	Stenatherina honoriae (Ogilby)	Estuarine hardyhead
Mugilidae	*Mugil cephalus* Linnaeus	Sea mullet
	Liza argentea (Quoy & Gaimard)	Flat-tail mullet
	Myxus elongatus Gunther	Telegalene
	Trachystoma petardi (Castelnau)	Freshwater mullet
Carangidae	*Seriola hippos* Gunther*	Samson fish
	Trachurus declivis (Jenyns)	Yellowtail
	Usacaranx nobilis Macleay	Trevally
	Alectis ciliaris (Bloch)	Pennant fish
Pomatomidae	*Pomatomus saltator* (Linnaeus)	Tailor
Leiognathidae	*Equulites moretonensis*	Spotted ponyfish
Apogonidae	*Lovamia fasciata* (White)	Soldier fish
	Adenopogon cephalotes (Castelnau)	Slender gobbleguts
Ambassidae	*Velambassis jacksoniensis* (Macleay)	Glassy perchlet
Moranidae	*Percalates colonorum* (Gunther)	Estuary perch
Theraponidae	*Pelates sexlineatus* (Quoy & Gaimard)	Trumpeter
	Therapon servus (Bloch)	Crescent perch
Sparidae	*Chrysophrus auratus* (Bloch & Schneider)	Squire, snapper
	Rhabdosargus sarba (Forskål)	Tarwhine
	Mylio australis (Gunther)	Black bream

TABLE 1 (*Continued*)

Family	Species	Common Name
Girellidae	*Girella tricuspidata* (Quoy & Gaimard)	Luderick
Enoplosidae	*Enoplosus armatus* (White)	Old wife
Gerridae	*Gerres ovatus* Gunther	Silverbelly
Mullidae	*Upeneichthys porosus* (Valenciennes)	Blue-striped red mullet
	Upeneoides tragula (Richardson)	Surmullet
Sciaenidae	*Sciaena antarctica* Castelnau	Mulloway (jewfish)
Sillaginidae	*Sillago maculata* Quoy & Gaimard	Trumpeter whiting
	Sillago ciliata (Valenciennes)	Sand whiting
Cheilodactylidae	*Nemadactylus macropterus* (Bloch & Schneider)	Morwong
	Cheilodactylus fuscus Castelnau	Red morwong
	Goniistius gibbosus (Richardson)	Magpie morwong
Scorpidae	*Actypichthys mado* Whitley	Mado
Monodactylidae	*Monodactylus argenteus* (Linnaeus)	Silver batfish
Scatophagidae	*Selenotoca multifasciata* (Richardson)	Butterfish
Chaetodontidae	*Microcanthus joyceae* Whitley	Stripey
Acanthuridae	*Prionurus microlepidotus* Lacepède	Plain surgeonfish
Siganidae	*Amphacanthus nebulosus* Quoy & Gaimard	Black trevally
Scorpaenidae	*Notesthes robustus*	Bullrout
	Centropogon australis	Fortesque
Platycephalidae	*Planiprora fusca* (Valenciennes)	Dusky flathead
	Trudis caeruleopunctatus (McCulloch)	Sand flathead
	Suggrundus jugosus (McCulloch)	Black-backed flathead
Triglidae	*Currupiscus volucer* Whitley	Red gurnard
Coridae	*Pseudolabrus cyprinaceus* (White)*	White spotted parrotfish
	Achoerodus gouldii (Richardson)	Blue groper
Eleotridae	*Philypnodon grandiceps* (Krefft)	Flat-headed gudgeon
	Carassiops compressus (Krefft)	Carp gudgeon
	Bathygobius krefftii (Steindachner)	Krefft's goby
	Callogobius mucosus (Gunther)	Slimy goby
	Arenigobius frenatus (Gunther)	Bridled goby
	Cryptocentrus cristatus (Macleay)	Crested goby
	Paraphya semivestita (Munro)	Transparent goby
	Redigobius microphthalmus (Gunther)	Small-eyed goby
	Favonigobius obliquus (McCulloch & Ogilby)	Spotted goby
Blenniidae	*Dasson steadi* Whitley	Sabre-toothed blenny
Clinidae	*Cristiceps australis* Valenciennes	Weedfish
	Cristiceps auranticus Castelnau	Crested weedfish
Callionymidae	*Foetorepus calauropomus* (Richardson)	Dragonet
Uranoscopidae	*Ichthyscopus lebeck* (Bloch & Schneider)	Stargazer
Monacanthidae	*Monacanthus chinensis* (Osbeck)	Centreboard
	Meuschenia trachylepis (Gunther)	Yellow-finned leatherjacket
	Scolinichthys granulatus (White)	Rough leatherjacket
	Eubalichthys mosaicus (Ramsay)	Mosaic leatherjacket
	Brachaluteres fidens Whitley	Pigmy leatherjacket
Tetraodontidae	*Spheroides hamiltoni* (Gray & Richardson)	Common toado
	Spheroides pleurogramma (Regan)	Gold-banded toado
	Ovoides aerostaticus (Jenyns)	Balloon fish
Diodontidae	*Dicotylichthys punctulatus* Kaup	Porcupine fish
	Diodon holocanthus (Linnaeus)	Tropical porcupine
Antennariidae	*Antennarius commersonii* (Cuvier)	Black angler
	Phrynelox striatus (Shaw)	Striped angler
	Histrio histrio (Linnaeus)	Marbled angler

Two species which have been recorded from Lake Macquarie were not collected during the course of this study. They are *Parapegasus natans* (L.), recorded by McCulloch (1927), and the Australian salmon, *Arripis trutta* (Bloch & Schneider), a southern migratory fish which is recorded from the lake a number of times in the annual reports of the New South Wales Department of Fisheries, the last occasion being 1949.

Notable absentees from the lake are sharks of all kinds (though they occur in the lower entrance channel at times, and in 1957 one was reported to have attacked a horse in the lake). The whaler, *Carcharinus spenceri* (Ogilby), and the estuary stingaree, *Dasyatis fluviorum* Ogilby, are common elements of the fauna of the estuaries in this region but were not taken in the lake. Within the lake the common stingray, *Urolophus testaceus*, was abundant on the sandy bottoms near the entrance channel. There is only slight freshwater run-off into the lake (Baas Becking, Thomson, and Wood 1959, Spencer 1959) and therefore there is no intrusion of freshwater fauna. There has been only one record of a freshwater mullet (*Trachystoma petardi*) occurring in the lake.

III. The Food of the Fishes

(*a*) *The Sampling*

The species were sampled, and the contents of the stomachs of individuals were examined, in numbers roughly corresponding to their abundance. The stomachs taken in the field were preserved in formalin and inspected later in the laboratory. Only identification of the food organisms was attempted, as the objections to assigning any significance to volume or weight measurements of food expressed by Thomson (1957) apply here. There are no records of the food of the 21 species listed below:

Aseroggodes macleayanus
Atypichthys mado
Brachaluteres fidens
Carassiops compressus
Cryptocentrus cristatus
Equulites moretonensis
Fistularia petimba
Gambusia affinis
Heterodontus portusjacksoni
Lovamia fasciata
Ovoides aerostaticus
Paraphya semivestita
Philypnodon grandiceps
Scolenichthys granulatus
Seriola hippos
Stigmatopora argus
Suggrundus jugosus
Trachystoma petardi
Trudis caeruleopunctatus
Upenichthys porosus
Yozia tigris

(*b*) *Classification of Feeding Types*

The fish have been classified into various groups according to the nature of their food. A distinction is made between microphagous and macrophagous carnivores, because only the latter are likely to feed directly on the older age groups of commercial fish and Crustacea.

(c) *The Herbivores*

Eight species of fish recorded from Lake Macquarie have been classed as herbivores (Table 2). Recognizable animal remains were observed in the stomach contents of fewer than 1 per cent. of these species. These remains were generally of harpacticoid copepods which are common amongst filamentous algae. It is probable that their consumption was accidental and it is reasonable to suppose that animal substance plays little part in the nutrition of these fish. Three species, *Girella tricuspidata*, *Mugil cephalus*, and *Hemirhamphus ardelio* are of commercial importance, and a fourth, *Selenotoca multifasciata*, is also large enough to be eaten, but it occurs in small numbers. The first three species consumed the same food but took the individual food organisms in different proportions. *Zostera* dominates in the diet of the garfish, *Hemirhamphus ardelio*; filamentous algae in the diet of *Girella tricuspidata*; and diatoms in that of *Mugil cephalus*. The animal material found is also recorded in Table 2 but as mentioned above this was never in such quantity as to indicate deliberate feeding on animals.

TABLE 2

THE FOOD ORGANISM TYPES OF THE HERBIVOROUS FISHES OF LAKE MACQUARIE

M, major food item in over 80 per cent. of stomachs; *m*, major food item in less than 20 per cent. of stomachs or present as a minor item only; *o*, occasionally present

Species	Diatoms	Algae	Blue–Green Algae	Zostera	Amphipods and Copepods	Forams
Amphacanthus nebulosus	*M*	*M*			*o*	
Eubalichthys mosaicus	*M*	*m*				
Girella tricuspidata	*m*	*M*	*m*		*o*	
Monodactylus argenteus	*m*	*M*			*o*	*o*
Mugil cephalus	*M*	*m*	*m*		*o*	*o*
Prionurus microlepidotus	*m*	*M*				
Hemirhamphus ardelio	*m*	*m*		*M*		
Selenotoca multifasciata	*m*	*M*			*o*	

(d) *The Omnivores*

There are 13 species of fish from Lake Macquarie which are classed as omnivores (Table 3). *Usacaranx nobilis* is rather different from the others in that it devours fair-sized fish, and to judge by the bait it will accept, also eats molluscs and polychaet worms. These last two were not found in the few stomachs inspected. However, the amount of algal material was considerable and for that reason this species is classed as an omnivore rather than a carnivore. The tarwhine studied were fairly young, mostly in the 16–21 cm length group; no fish were found in their diet but quite large prawns were present. The polychaets taken by the tarwhine were often larger than those taken by most omnivores.

TABLE 3

THE FOOD TYPES OF THE OMNIVORES OF LAKE MACQUARIE

M, Major food item in over 80 per cent. of stomachs; *m*, major item in less than 20 per cent. of stomachs or present as a minor item only

Species	Diatoms	Algae	Zostera	Crustacea	Fish	Gastropoda	Pelecypoda	Polychaeta	Forams	Bryozoa
Achaerodus gouldii	*M*			*M*						
Arenigobius frenatus	*M*	*m*		*m*	*m*	*m*	*m*			
Dasson steadi	*M*	*M*		*m*						
Liza argentea	*M*	*M*		*M*			*m*		*m*	
Meuschenia trachylepis	*m*	*M*	*m*	*m*		*m*	*m*	*m*	*m*	*M*
Microcanthus joyceae	*M*							*M*		
Monacanthus chinensis	*m*	*M*	*m*	*M*		*m*	*M*	*m*		*m*
Pelates sexlineatus	*m*	*m*		*M*		*M*	*M*	*m*		
Hemirhamphus australis		*M*		*M*						
Rhabdosargus sarba	*m*	*M*	*m*	*m*		*m*	*m*	*M*	*m*	*m*
Spheroides hamiltoni	*m*	*m*	*m*	*m*		*M*	*M*	*m*		*m*
Stigmatopora nigra	*M*			*M*						
Usacaranx nobilis		*M*	*m*		*M*					

The groups Crustacea, Polychaeta, Gastropoda, etc. cover a variety of forms from diverse habitats. The groupings are given as such to indicate the type of food preferred. Except for *Rhabdosargus sarba* which takes prawns, and *Usacaranx nobilis* which takes fish, all the omnivores ingest small food materials, and all except *Usacaranx nobilis* and *Microcanthus joyceae* include copepods as important items in the diet. Most of these are harpacticoids of the type found on and about seaweeds; planktonic copepods were rarely present. The polychaets come from three main habitats; those from sandy bottoms are taken by *Spheroides hamiltoni*; the errant or tubicolous types from the seaweed or epizoic on rocks, mussel clumps, etc. form the food of the majority; and the polychaets of the mud zone, mainly *Maldane* sp., were found in two of the omnivores, *Pelates sexlineatus* and *Rhabdosargus sarba*, though relatively rarely in the former case. The distinctive limy tubes of the polychaet *Spirorbis* sp. occurred in some quantity in the stomachs of *Meuschenia trachylepis*, *Monacanthus chinensis*, and *Spheroides hamiltoni*. The consumption of *Zostera*

TABLE 4

THE FOOD OF THE MICROPHAGOUS FISHES OF LAKE MACQUARIE

M, Major item in over 80 per cent. of stomachs; *m*, major item in less than 20 per cent. of stomachs or present as minor item

Species	Crustacea	Mollusca	Polychaeta	Forams	Fish Larvae
Achlyopa nigra	*M*	*m*	*M*		
Adenopogon cephalotes	*M*				*M*
Bathygobius krefftii	*M*	*M*	*M*		
Callogobius mucosus	*M*		*M*		
Centropogon australis	*M*	*m*	*m*		
Cristiceps auranticus			*M*		
Cristiceps australis	*M*		*M*		
Favonigobius obliquus	*M*		*M*		
Galaxias attenuatus	*M*				
Gerres ovatus	*M*	*m*	*M*	*m*	*m*
Goniistus gibbosus	*M*				
Harengula abbreviata	*M*				
Hippocampus whitei	*M*				
Hyperlophus vittatus	*M*				
Muraenichthys australis			*M*		
Myxus elongatus	*M*	*m*	*m*	*m*	
Notesthes robustus	*M*		*M*		
Ophisurus serpens			*M*		
Plotosus anguillarus	*M*	*M*			
Pranesus ogilbyi	*M*				
Pseudolabrus cyprinaceus	*M*				
Redigobius microphthalmus	*M*		*m*		
Sardinops neopilchardus	*M*				
Spheroides pleurogramma	*M*				
Stenatherina honoriae	*M*				
Taeniomembras microstoma	*M*				
Urocampus carinirostris	*M*				*m*

by these species may be solely for the sake of the attached bryozoa as they were present on practically all *Zostera* pieces taken in the stomachs of these three species.

In most cases the pelecypods and gastropods mentioned were the very small species, or newly settled young of larger species which are common among the weeds and pebbles of the weed zone. Mussels which are typical of the slope zone (MacIntyre 1959) were found only in the stomachs of *Spheroides hamiltoni* which however also feed in the higher weed zone as evidenced by *Zostera*, *Ruppia*, and algae.

TABLE 5

THE FOOD OF THE MACROPHAGOUS FISHES OF LAKE MACQUARIE

M, Major item in over 80 per cent. of stomachs; *m*, major item in less than 20 per cent. of stomachs or present as minor item

Species	Fish	Prawns	Crabs	Small Crustacea	Mollusca	Polychaeta
Alectis ciliaris	*M*			*M*		
Anguilla australis	*M*	*m*				
Antennarius commersonii	*M*	*M*				
Centroberyx affinis	*M*	*m*				
Cheilodactylus fuscus	*M*					*m*
Chrysophrys auratus	*m*			*M*		*M*
Cnidoglanis macrocephalus		*m*		*m*	*M*	*M*
Currupiscus volucer	*M*	*m*				
Dicotylichthys punctulatus			*m*		*M*	*m*
Enoplosus armatus		*M*		*m*		*m*
Foetorepus calauropomus		*m*		*M*		*M*
Histrio histrio	*M*	*M*				
Ichthyoscopus lebeck	*M*	*M*		*m*		
Lhotskia macleayana	*M*	*m*				
Mylio australis	*m*	*M*	*m*	*m*	*M*	*M*
Nemadactylus morwong	*M*	*m*				
Percalates colonorum		*M*				*M*
Phrynelox striatus	*M*					
Planiprora fusca	*M*	*M*	*m*			
Pomatomus saltator	*M*	*m*				
Pseudorhombus jenynsi	*m*	*M*	*M*			
Sciaena antarctica	*M*		*m*			
Seriola hippos	*M*	*m*				
Sillago ciliata	*m*	*m*	*m*	*M*	*m*	*M*
Sillago maculata	*m*	*m*		*M*		*M*
Therapon servus	*M*					
Trachurus declivis	*M*					
Trachynocephalus myops	*M*	*M*				
Upeneichthys tragula		*M*		*m*	*m*	*M*
Urolophus testaceus		*M*	*m*			*M*
Zeus faber	*M*					

Monacanthus chinensis takes small crabs or crab limbs when it can, and *Spheroides hamiltoni* feeds on crab megalopae when available.

(e) *The Carnivores*

Most fish species in Lake Macquarie are carnivores: 31 are macrophagous and 27 microphagous (Tables 4 and 5).

Some of the microphagous species appear to feed solely on crustacean food, and others only on polychaets. None of the other types of food taken appear to be the sole food for any species. Apart from the three species shown in Table 4 not to consume any crustacean food, all the others, except three, consume copepods. The three exceptions are *Pseudolabrus cyprinaceus*, which took amphipods, and *Adenopogon cephalotes* and *Urocampus carinirostris*, which feed on the sergestid shrimp, *Acetes australis* Colefax.

TABLE 6

FISH FEEDING UPON PLANKTON IN LAKE MACQUARIE

Purely or Mostly Planktivorous	Occasionally Planktivorous
Engraulis australis	*Alectis ciliaris*
Goniistius gibbosus	*Chrysophrys auratus*
Harengula abbreviata	*Galaxias attenuatus*
Hyperlophus vittatus	*Gerres ovatus*
Sardinops neopilchardus	*Hippocampus whitei*
Stenatherina honoriae	*Velambassis jacksoniensis*

Amphipods, ostracods, and crab megalopae are taken at times by most species. Cladocera have been recorded from the stomachs of only *Gerres ovatus*, *Hyperlophus vittatus*, *Myxus elongatus*, and *Velambessis jacksoniensis*.

All but six of the macrophagous species consume fish either as a major or minor part of the diet. It is probable that *Percalates colonorum* also consumes fish though none were taken from stomachs during this investigation. The kind of fish consumed varies according to the habits of the predator. *Pomatomus saltator* take mostly hardyhead, either *Stenatherina honoriae* or *Pranesus ogilbyi*, with an occasional mullet. *Planiprora fusca* and *Anguilla australis* consume mullet, mainly *Liza agentea*, besides quantities of gobies. Gobies seem to comprise the greater part of the fish food of the other piscivorous species. The quite abundant *Pelates sexlineatus* was taken in the stomachs of several bream.

Besides the food organisms listed in Table 5 a few others were consumed by individual species. In some parts of the lake *Sillago maculata* were found to be feeding on ophiuroids. Heart urchins were found in the stomachs of some *Dicotylichthys punctulatus* taken on the sand flat near Pelican Island. *Chrysophrys auratus* were frequently taken with the polychaet *Maldane* sp. typical of the deepwater mudzone, but others were taken with planktonic copepods and chaetognaths. *Cnidoglanis macrocephalus* were found to consume jellyfish and foraminifera at times. *Mylio australis* were sometimes taken with bryozoa and sessile tunicates in the stomach.

(*f*) *The Plankton Feeders*

These are mainly carnivores and have been listed in Tables 4 and 5; however, as they are the only fish species to exploit directly this source of food supply they are mentioned especially here (Table 6). All seem to be selective, as frequently only one from among several local plankton forms was found in the stomachs (Kott 1955); *Hyperlophus vittatus* and *Velambassis jacksoniensis* both select cladocera. *Gerres ovatus* also takes cladocera besides other crustacea. So far chaetognaths have been seen only in *Chrysophrys auratus*. Also unique in its food as found in specimens from Lake Macquarie is *Engraulis australis*, all the specimens of which contained only dinoflagellates and mollusc larvae. The remainder of the planktivorous fish consumes mostly copepods which are the dominant forms in the plankton (Kott 1955). Some of the fishes recorded under the heading of omnivorous or microphagous may also feed on plankton to some extent, but the dominant copepods etc. in their stomachs are those typically found among the algal beds.

(*g*) *Relation to Benthic Food Supply*

As fish are mobile they can pass readily from one zone to another, but the majority of species obtain their food in one type of habitat. The herbivores feed solely in the weed zone. All the omnivores feed in the weed zone, but three species, *Spheroides hamiltoni*, *Pelates sexlineatus*, and *Rhabdosargus sarba* also commonly feed in the slope zone; the last two of these also forage in the mud zone. The microphagous carnivores are typical of the weed zone, though the polychaet eaters extend their feeding into the slope zone on occasions. The macrophagous carnivores are typical of the slope zone, though all make forays into the weed zone, and two, *Sillago maculata* and *Chrysophrys auratus*, also feed in the mud zone. The planktivorous fish and the larger fish eaters are largely independent of the benthic zonation and seek their food in the open water over any of the benthic zones.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

X. THE MOVEMENTS OF FISH

By J. M. Thomson*

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Summary

Of 20,128 fish of 29 species tagged, 9·4 per cent. were recovered by commercial fishermen and anglers. A further 1·5 per cent. were retaken by the tagging crew. Only 11 species were tagged in numbers greater than 100. Returns covered 17 species, showing recovery rates varying from 1 to 21 per cent.

Some exchange of fish takes place between the northern and southern parts of the lake, but this is consistent only in the case of the flat-tail mullet. Within the two parts of the lake lateral movements of some species take place; other species are sedentary. These facts suggest that the necessary condition for population estimation, that tagged fish should be randomly distributed amongst the population, is not achieved for most species.

I. Introduction

A tagging programme, which it was hoped would provide an estimate of the size of the stock of commercial fish in Lake Macquarie, was also designed to answer three questions; firstly, whether fish tagged in a certain spot were likely to become randomly distributed throughout the lake; secondly, whether there was free movement of fish between the northern and southern portions of the lake; and thirdly, the extent of emigration from the lake. A related problem, the extent of immigration of fish into the lake, could not be attempted with the resources available.

II. Methods

(*a*) *Tagging Procedure*

Marking was done by the attachment of numbered tags to the fish. At first three types of tag were used, a round plastic Petersen disk, the Lea hydrostatic tag, and a monel metal operculum strap tag (Anon. 1953). After the first 12 months only the operculum tag was used because returns were consistent with this type and examination of recaptured specimens bearing the other types revealed injury to the tissues. The operculum tag also has the advantage of being more rapidly applied than the other types. The strap tag was also used on two species of monacanthid, *Monacanthus chinensis* (Osbeck), and *Meuschenia trachylepis* (Gunther), species whose operculum opening is too small for insertion of a tag, by attaching the tag to the loose fold of skin immediately behind the ventral spine.

Tagging was carried on at a number of sites around the lake and various methods were used to obtain fish, including hauling nets, mesh nets, commercial

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beach seines, an otter (prawn) trawl, and a series of four shore traps. After capture the fish were held in the water except during the tagging and measuring procedures. Only lively fish were tagged.

TABLE 1

NUMBERS OF FISH TAGGED AND NUMBERS RECAPTURED, LAKE MACQUARIE, 1954–58

The scientific names of these fish are given in Thomson (1959, Table 1)

Species	Number Tagged	Number Retaken	Total Percentage Retaken	Retaken by Anglers (% of Total)	Experimental Recaptures
Black bream	2281	141	6·2	11·3	19
Butterfish	20	4	20·0	50·0	0
Centreboard	512	110	21·5	2·7	3
Dusky flathead	97	11	11·3	54·5	1
Estuary perch	70	4	5·7	0	1
Flat-tail mullet	3934	155	3·9	42·6	66
Flounder	116	0	0	0	1
Freshwater mullet	1	0	0	0	0
Jewfish	12	0	0	0	0
Leatherjacket	1256	158	12·6	24·1	64
Long tom	3	0	0	0	0
Luderick	1331	63	4·7	46·0	3
Morwong	3	1	33·3	0	0
Nannygai	12	1	8·3	0	0
Oldwife	22	0	0	0	1
Pennant-fish	1	0	0	0	0
Red gurnard	6	0	0	0	0
Sand whiting	83	1	1·2	0	1
Sea mullet	3163	161	5·1	29·8	16
Squire	3783	718	18·9	29·2	42
Stingaree	28	0	0	0	0
Surmullet	2	0	0	0	0
Tailor	200	5	2·5	40·0	0
Tarwhine	2515	340	13·5	20·9	24
Telegalene	172	3	1·7	66·6	0
Trevally	206	23	11·2	39·1	0
Trumpeter	75	2	2·7	100·0	0
Trumpeter whiting	149	0	0	0	0
Yellowtail	82	0	0	0	0
All species	20128	1901	9·4	26·6	242

(*b*) *Recapture Procedure*

Publicity concerning the programme was arranged as recapture of tagged fish depended upon recognition and return by commercial fishermen and by anglers. Some few were sighted by cleaners at Newcastle and Sydney markets, and one or two were even returned from fish shops. Besides these, the tagging crew recaptured a certain number of fish, mostly in the traps. These latter fish were released after the tag number had been checked and the fish measured. Wherever possible the fish retaken by fishermen were measured by a member of the tagging crew, but some tags were returned without the fish. Some fish were tagged in July and September 1953, but regular sampling commenced in January 1954 and continued until February 1956. Tags have been returned up to April 1958.

TABLE 2

FREQUENCY OF RETURN OF TAGS IN 10-DAY PERIODS UP TO 100 DAYS FROM TAGGING

Species	Days from Tagging										
	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	Total (%)
Bream	10	4	11	9	15	5	7	9	9	8	61·7
Centreboard	33	28	10	4	5	4	3		4	2	84·5
Esturary perch	1				1					1	75·0
Flathead	1			1	1	1					36·3
Flat-tail mullet	9	4	5	7	6	7	1	8	5	5	36·8
Luderick	8	6	7		1	3	2	2			46·0
Leatherjacket	25	24	6	9	6	7	13	11	9	10	75·9
Nannygai	1										100
Sea mullet	6	6	14	3	4	3	5	2	2		27·9
Squire	41	113	132	33	114	52	42	40	16	19	83·8
Tailor	1			3					2		85·7
Trumpeter				1	1						100
Trevally	4	4	3		1		1	1	1		71·4
Tarwhine	28	31	30	31	22	24	32	23	17	15	75·0
Total	168	220	218	101	177	106	106	96	65	60	69·3

III. RESULTS

(*a*) *The Proportion of Recaptures*

In Table 1 are shown the numbers of fish of each species tagged and the numbers returned. 9·4 per cent. of all fish tagged were returned by fishermen. The 242 tagged fish retaken by the experimental team are not included in the percentage retaken as they were all returned to the water except two which had become gilled in nets and were killed. These are not included in the 20,128 shown.

No tagged specimens of 11 species were recaptured. These were all tagged in relatively few numbers, though over 100 each of flounder and trumpeter whiting were tagged. Of the remaining 17 species returns ranging from 1 to 21 per cent. are recorded (ignoring the 33·3 per cent. return for morwong which represents one return from three tags). These figures include all returns made over a period of 4 years, and so do not represent fishing rates. Tables 2 and 3 record the frequency of return of tags in successive periods.

Except for three species, sea mullet, flat-tail mullet, and luderick, more than half the returns were made within 100 days of the fish being tagged. Only 40 per cent. of the returns were made after the first year. The greatest number of returns in any 10-day period were made in the first 10 days except in the case of bream, sea mullet, squire, and tarwhine. More of these species were retaken during the

TABLE 3

FREQUENCY OF RETURN OF TAGS AFTER 100 DAYS FROM TAGGING

Species	Days from Tagging											
	100+	150+	200+	250+	300+	400+	500+	600+	700+	800+	900+	1000+
Bream	13	15	10	7	2			1	3			
Butterfish	1											
Centreboard	4	2	1		1	1			1			
Flathead			2	2	1	1					1	
Flat-tail mullet	24	18	16	8	6	6	2	1				
Luderick	4	8	8	6	2	1		1	1			
Leatherjacket	12	5	7	8	19	14						
Sea mullet	15	16	9	8	19	13	13	7	5	2		
Squire	49	29	14	5	5				1			
Telegalene				1								
Trevally	4	2			1							
Tarwhine	37	22	10	7	1				1			

TABLE 4

RETURN OF TAGS DURING THE FIRST 10 DAYS AFTER TAGGING

Species	Days from Tagging										
	0	1	2	3	4	5	6	7	8	9	10
Bream		4		3					1	2	
Centreboard				7	4	10	2	2	2	3	3
Esturary perch				1							
Flathead			1								
Flat-tail mullet		1	2		3		1		1	1	
Luderick					1	1		1		3	2
Leatherjacket	1	3	1	4	1	5	1	4	2	2	1
Nannygai						1					
Sea mullet			1	2		1	2				
Squire		9		1	2	6	1	15	2	3	2
Trevally			1					1	2		
Tarwhine	1	2	4			3	1	12	1	2	2

second and third 10-day periods, except for bream whose returns were low in the second 10-day period and whose greatest returns were in the 41–50 day period.

These results suggest that at least in the case of these species any method of estimating mortality rates or population numbers from daily tag returns, as in

Schnabel's (1938) method, would be inaccurate for the first few days. The lower early return compared with later recaptures may indicate that there is some shock reaction which makes the fish less liable to be recaptured during the first few days.

Two tagged fish were recaptured the same day as they were tagged, one in a hauling net, the other on a hook. The number of recaptures does seem to increase after 5–7 days (Table 4). The gradual decrease in the number of returns (Tables 2 and 3) could be due in part to mortality. Another cause of loss would be departure of fish from the lake. It is a matter of observation that fish schools do enter and leave the lake through the entrance channel, but the only direct evidence is from relatively few tagging returns.

The tagging crew retook, either in the traps or in nets, 242 tagged fish of 13 species. This includes 12 leatherjackets which were retaken twice, but does not include one particular leatherjacket which was taken more than a dozen times over several months in the trap at the entrance to the channel (Table 5).

The large number of recoveries of flat-tail mullet within a week of tagging reflects re-entry into the shore-line traps soon after release. This, together with the large number of this species caught in the traps, indicates that the flat-tail mullet, at least at times, move close along the shore. The number taken is in strong contrast with the number of sea mullet taken, and this presumably reflects different habits; the flat-tail mullet moving laterally along the shore, while the sea mullet tend to move on to the flats from the deeps more or less vertically to the shoreline and then retire to the deeper channels after feeding.

(*b*) *Movements between North and South*

The tagging recaptures suggest that there is some movement of fish between the two halves of the lake (Table 6). This is most marked in the case of flat-tail mullet (Fig. 1). The recaptures of fish tagged in the entrance channel indicate that there is no favoured or environmentally imposed direction of movement on entry into the lake. However, if there were such a movement it would become obscured by subsequent movements. The centreboards which were recaptured in relatively large numbers showed no evidence of movement between the two parts of the lake. There is no evidence of movement of flathead, tailor, and perch, but these were tagged and recaptured in far fewer numbers. Excluded from Table 6 are those species which were tagged or returned in few numbers. From the available evidence (Figs. 2 and 3) leatherjackets and squire moving from south to north do not pass far north of the inner end of the entrance channel.

There is some evidence that flat-tail mullet are continually on the move around the shallows of the lake. This species was caught more abundantly than any other in the shore-line traps. A few days after tagging they have been recaptured considerable distances from the tagging point; this is in strong contrast with some of the species mentioned in the next section. One fish moved from Galgabba to Cockle Creek in 2 days and another from Wangi to Marwong Point in the same time (Fig. 1). Three flat-tail mullet tagged in May 1954 at Galgabba were later retaken at Morisset in company with nine others which were tagged in the interim period, one at the end of May also at Galgabba, two in June at Valentine, and in

TABLE 5

FREQUENCY OF RECAPTURE OF TAGGED FISH BY EXPERIMENTAL TEAM

Species	Days from Tagging											
	0–10	11–20	21–30	31–40	41–70	71–100	100+	200+	300+	400+	500+	Total
Bream	6	2	4		3	3			1			19
Centreboard			2				1					3
Estuary perch		1										1
Flathead					1							1
Flat-tail mullet	32	3	5	4	11	2	5	4	1			67
Flounder							1					1
Luderick	1	1					1					3
Leatherjacket	18	21	4	6	12	2	1					64
Oldwife						1						1
Sea mullet	3	4	3		2	2		1			1	16
Squire	11	13	7	4	2	3	2					42
Sand whiting						1						1
Tarwhine	8	5	8	2								23
Total	79	50	33	16	31	14	11	5	2		1	242

TABLE 6

NUMBER OF FISH TAGGED IN THE NORTHERN OR SOUTHERN PARTS OF LAKE MACQUARIE AND THE AREA OF RECAPTURE

This includes fishes listed in both Table 1 and Table 5. Discrepancies in the totals are due to recoveries of fish outside Lake Macquarie

Species	Tagged in North			Tagged in South			Tagged in Entrance			
	Number	Recaptured		Number	Recaptured		Number	Recaptured		
		North	South		South	North		North	South	Entrance
Bream	308	4	1	1972	154		1		1	
Butterfish	16	3	1	4	0		0			
Centreboard	103	3		396	110		3			
Dusky flathead	32	0		58	12		7			1
Eastuary perch	10	0		49	9		11	3	3	
Flat-tail mullet	1918	55	30	1884	51	38	132	1	2	
Leatherjacket	350	20	2	845	187	6	61	1	3	3
Luderick	578	14	5	719	46	1	34	3	1	
Sea mullet	1997	84	23	1003	43	7	163	6	10	1
Squire	92	3		3694	746	11				
Tailor	14			186	5					
Tarwhine	125	3	3	2390	349	8				
Telegalene	62	1		66	1	1	44			
Trevally	9		1	196	19	3	1			

August two at Valentine, one at Swansea, and three at Wangi. One of these was also taken at Morisset but released again in October. Other flat-tail tagged at Galgabba in May were also recaptured in June at Valentine on the day when those mentioned above were tagged. Two others tagged at Galgabba in May were taken at Valentine in August. There is in this at least some evidence that the fish of this species tend to remain together in schools. Assuming that this is so the facts given above could be interpreted to mean that a school at Galgabba in May had moved

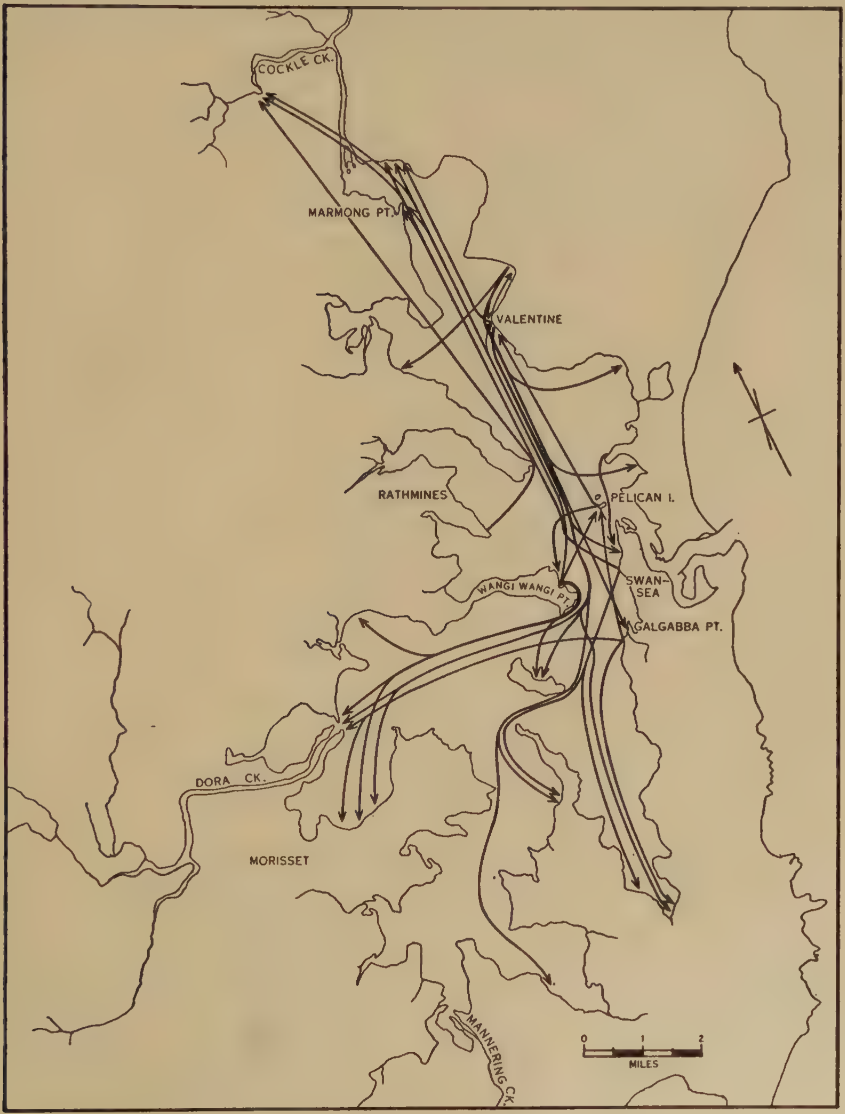
COCKLE CK.
MARMONG PT.
VALENTINE
RATHMINES
PELICAN I.
WANGI WANGI PT.
SWAN-SEA
GALGABBA PT.
DORA CK.
MORISSET
MANNERING CK.
0
1
2
MILES

Fig. 1.—Movements of flat-tail mullet in Lake Macquarie.

to Valentine in June, were either still at Valentine or had returned there in early August when they moved rapidly south to Swansea flats and then Wangi. Later, in November this school appeared near Morisset. There are several other cases of two or three flat-tail which were tagged together being recaptured in the same haul or trap some months later, strengthening the evidence that the schools tend to remain largely intact, or that at least some fish remain in association even if there is change in the bulk of the constituents of the schools.

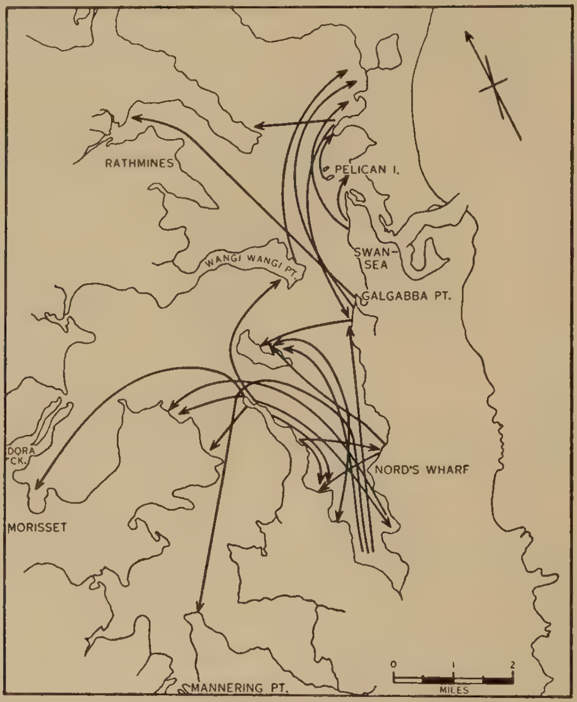

Fig. 2.—Movements of leatherjackets in Lake Macquarie.

There does not seem to be any such consistent movement of other species though considerable lateral movement does take place. This is shown for flat-tail mullet, leatherjacket, and squire in Figures 1–3 and for sea mullet in Figure 4. Similar patterns are shown by other species. The fact that most of the lateral movement shown in these figures is from east to west is due to more tagging being done along the eastern shores of the lake, not from choice but because consistently the tagging crew had better results there.

(*c*) *Sedentary Behaviour*

Certain species, notably the two monacanthids, the centreboard, and the yellow-fin leatherjacket, appear to be sedentary in habit (Table 7). The term sedentary is here used to denote the habit of moving around very little or in only a circumscribed area and is distinct from the term sessile with which it is sometimes confused, the latter term indicating physical attachment. This localization may be a form of territorial behaviour similar to that found in some birds and freshwater fishes but as no details of the habits are known the term sedentary is used. The returns were not the result of heavy fishing soon after tagging, as many were retaken after considerable periods (Table 7). One centreboard was taken 739 days after tagging still in the same position and a leatherjacket after 422 days. Several sea mullet were retaken at the tagging site more than 500 days after tagging, with one after 715 days. A flathead was taken after 929 days in the spot where it was tagged. There is probably room for doubt whether these latter two species are sedentary as they are known to migrate and the paucity of early recaptures from the tagging sites (Table 7) may indicate an emigration followed by a subsequent return.

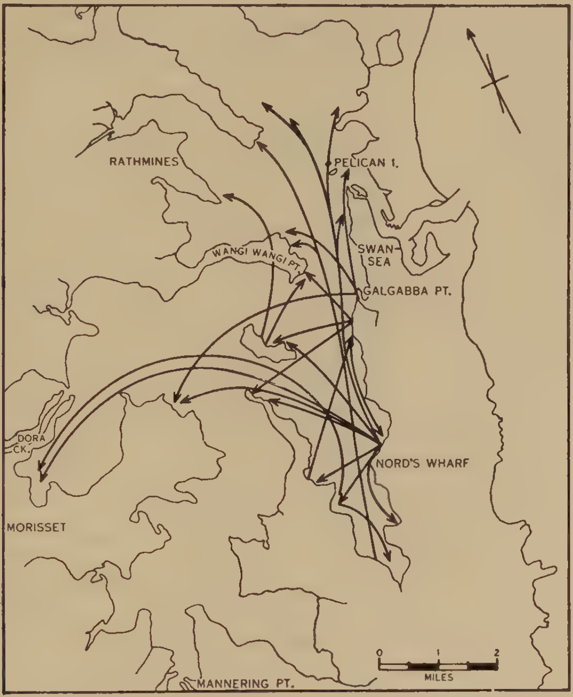

Fig. 3.—Movements of squire in Lake Macquarie.

Many centreboards, leatherjackets, and squire caught away from the tagging sites were on adjacent areas or between the tagging site and the entrance channel, indicating that they were moving on their migration from the lake when captured.

Besides these fish retaken by commercial fishermen or by anglers, all but 49 of the fish recaptured by the tagging crew (Table 5) were taken on the original tagging spot. The exceptions were mostly flat-tail mullet. However, as many of these recaptures were from the shore-line traps they could be the result of re-entry soon after tagging. One particular leatherjacket, however, was taken in the Pelican Island trap at the entrance channel 12 times although it was released in all directions from the trap. Several other leatherjackets were retaken two, three, or four times in the particular trap in which they were first taken.

(*d*) *Migration from the Lake*

Direct evidence of movement from the lake is provided by tagging; 47 tagged fish (2·5 per cent. of total tag returns) were recaptured outside the lake. Of these, 32 were sea mullet, which are well known to carry out extensive migrations along the coast (Thomson 1955). Of the other species taken outside the lake there were four each of luderick and yellow-fin leatherjackets, two each of flat-tail mullet and tarwhine, and one each of tailor, trevally, and squire. Of the others there is probably at least some movement between estuaries, and certainly the predominantly sea-inhabiting red gurnard, pennant-fish, nannygai, morwong, long tom, and jewfish can be regarded as only visitors to the estuaries.

TABLE 7

FREQUENCY OF RECAPTURE OF TAGGED FISH ON THE SAME GROUNDS AT SPECIFIED PERIODS AFTER TAGGING

Species	Days from Tagging									Number	Per cent. of Total Recapture
	0–10	11–20	21–30	31–40	41–70	71–100	100+	200+	300+		
Bream	1	2	5	1	5	1	4	4		24	17
Centreboard	32	22	9	6	15	2	4	1	3	94	85
Flathead				1				1	2	4	36·4
Flat-tail mullet	1		1	1	1					4	2·6
Leatherjacket	20	20	6	5	16	11	3	3	1	86	54·4
Luderick		5			1	2	1	1		10	15·8
Morwong					1					1	100
Sand whiting							1			1	100
Sea mullet			1	1	2				21	25	15·5
Squire	31	99	100	19	99	32	31	2	2	415	57·8
Tarwhine	7	10	13	12	9	15	9	3	1	79	23·2
Telegalene							2			2	66·6
Trevally	3	1	1	1		1				7	30·4

The direction of movement from Lake Macquarie is of interest. The movement of sea mullet is known to be predominantly to the north (Kesteven 1953; Thomson 1955), and all 32 recoveries were to the north (Fig. 5), eight of them in southern Queensland, the most northerly recovery being at Tin Can Bay, 428 days after tagging. All but two of these recoveries were made during late summer and autumn, which covers the migration period of the sea mullet. The exceptions were taken in the Nambucca River, one in October, the other in December, but as they were retaken 551 and 828 days respectively after tagging they probably moved during the normal migration season.

The four leatherjackets were all taken to the north between Crowdy Head and Port Macquarie, in traps set some miles to sea. They were recaptured between the months of October and January. It is probably significant that each year the leatherjackets were available in large numbers for tagging in Lake Macquarie up to the middle of October, after which they were scarce for some months. This sug-

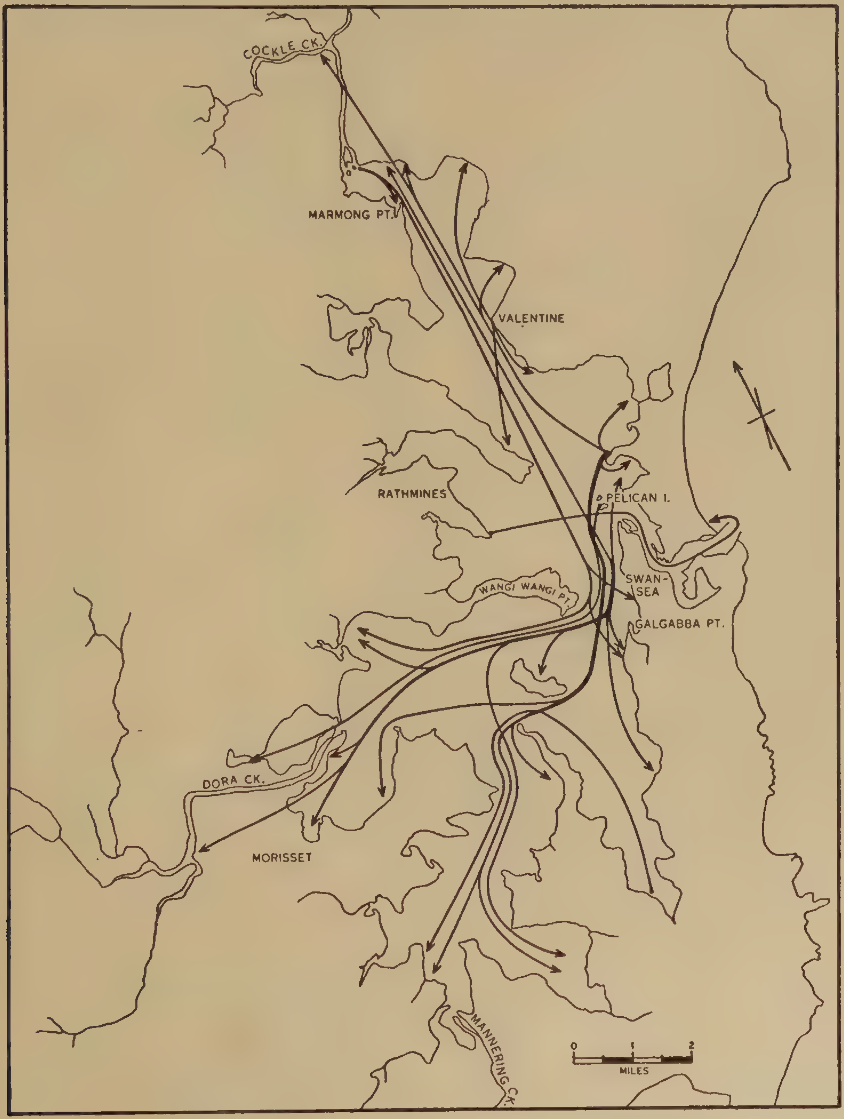
COCKLE CK.
MARMONG PT.
VALENTINE
RATHMINES
PELICAN I.
SWAN-SEA
GALGABBA PT.
WANGI WANGI PT.
DORA CK.
MORISSET
MANNERING CK.
0
1
2
MILES

Fig. 4.—Movements of sea mullet in Lake Macquarie.

gests that leatherjackets tend to leave the estuaries, presumably on a spawning migration in the late spring.

Two luderick were retaken to the south of Lake Macquarie, one being taken in Middle Harbour, Port Jackson, and another at the Cook's River breakwater in Botany Bay. However, the other two luderick were recaptured to the north, one at Laurieton, the other at Forster.

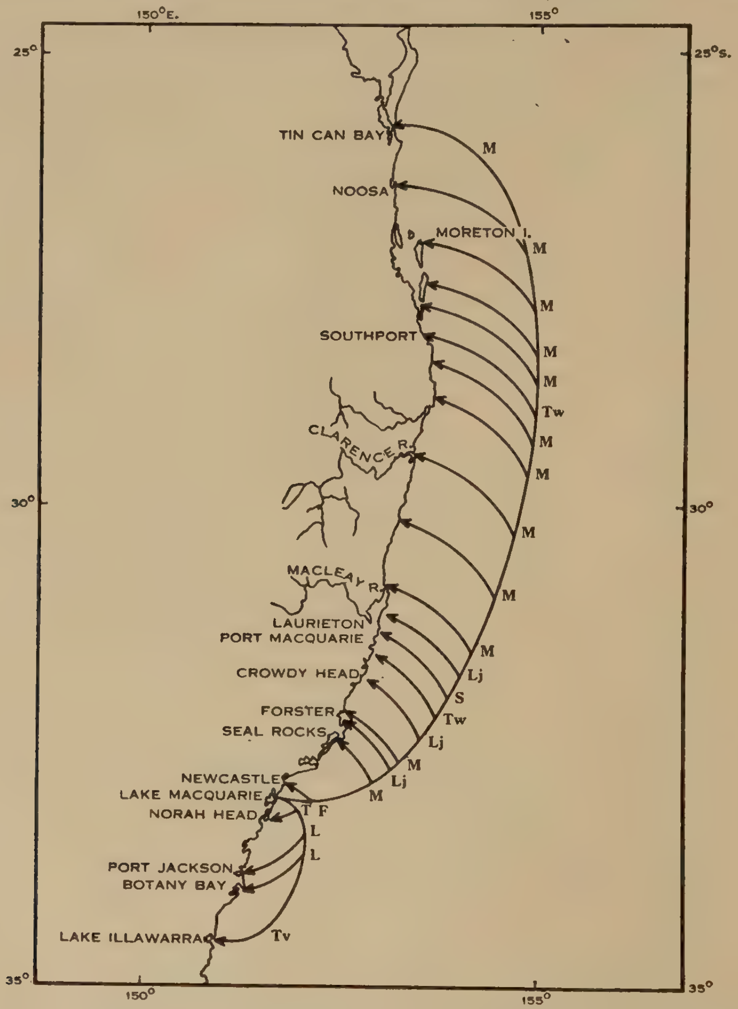
150°E.
155°
25°
25°S.
TIN CAN BAY
M
NOOSA
MORETON I.
M
M
SOUTHPORT
M
M
Tw
CLARENCE R.
M
M
30°
30°
M
MACLEAY R.
M
LAURIETON
PORT MACQUARIE
M
CROWDY HEAD
Lj
S
FORSTER
Tw
SEAL ROCKS
Lj
M
NEWCASTLE
Lj
LAKE MACQUARIE
M
NORAH HEAD
T F
L
L
PORT JACKSON
BOTANY BAY
LAKE ILLAWARRA
Tv
35°
150°
155°
35°

Fig. 5.—Migrations from Lake Macquarie. *F*, flat-tail mullet; *M*, sea mullet; *L*, luderick; *Lj*, leatherjacket; *T*, tailor; *S*, squire; *Tv*, trevally; *Tw*, tarwhine.

Other movements to the south were indicated by the single recaptures, a tailor at Norah Head and a trevally off the sea beach at Lake Illawarra.

The squire of estuaries are the young forms of the snapper of the sea reefs. The one proven example of movement to sea from Lake Macquarie was one taken in a snapper trap 7 miles to sea from Port Macquarie which is some 130 miles to the north of Lake Macquarie. One of the travelled tarwhine was also taken at Port Macquarie and the other even further to the north at Southport in southern Queensland.

IV. CONCLUSIONS

Although almost all species showed some movement between the northern and southern parts of the lake (Table 6), this took place at all seasons of the year only in the case of flat-tail mullet. Only this species therefore is likely to approximate the random distribution within the lake necessary for the proper use of tagging returns to estimate population numbers. Even for this species the tendency for the schools to remain as homogeneous units may nullify the randomness. In other words it is the school, not the individual, which moves more or less randomly about the lake.

Within the northern and southern portions of the lake there is lateral movement but the pattern of returns does not indicate that this is completely random dispersal. Centreboards, and to a somewhat lesser extent squire and leatherjackets, are sedentary and tagged fish do not become dispersed amongst the population. Emigration from the lake is proven directly only for eight species on the basis of tagging returns, and of these only sea mullet have been taken in large numbers.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

XI. ESTIMATION OF FISH POPULATIONS

By J. M. Thomson*

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Summary

Estimations of populations of six species of commercial fish were carried out by the mark-and-recapture method using modifications of the calculation methods of Petersen and Schnabel. Results from the two methods do not differ in order of magnitude except in occasional months. The estimates, however, are probably unreal, or refer to a part of the population rather than the whole, as it is doubtful whether tagged fish became randomly distributed throughout the population and migration and mortality must have continued during the period of calculation. It was possible to make an estimate of mortality rate but not of the effects of migration, nor of recruitment.

I. Introduction

Since the early formulations of Baranov (1918) and Russell (1931) a considerable number of papers have been written extending the theoretical basis of the methods of estimation of populations. Reviews of most of these are provided by Delury (1951) and Scattergood (1954). Published attempts to make use of these theoretical models are few. When the study reported here was being planned it was hoped that it would provide an example of the actual use of theory.

In result, the attempt demonstrates the large margin of error of the methods used when sampling is very small compared with either the population or the fish catch. This state of affairs is common to the majority of tagging experiments. The study is none the less useful, for it indicates the many problems which beset such attempts. Also, although the margin of error is considerable, that portion due to statistical error can, in most instances, be assessed and the maximum likely population of fish of marketable species estimated.

II. Methods

Estimates of population level were attempted by the mark-and-recapture method.

It was not feasible to make estimates by the use of catch-effort information as the catch figures were available only for intervals of 1 month which is in general too long a period to show a straight-line relationship between catch per unit of effort and accumulated catch. The principal disturbing factors are recruitment, immigration, and emigration.

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Marking was done by the attachment of numbered tags to the fish captured by various means (Thomson 1959*b*). Only data from professional fishermen were used in population estimates, as no means existed of estimating the anglers' catch.

The tagging data have been treated in two ways. Firstly, estimates of the Petersen type were made considering each month's tagging as a separate experiment and therefore giving a series of monthly estimates of population. Confidence limits were estimated by the method of Delury (1951). Secondly, Delury's (1951) modification of Schnabel's (1938) method was applied over the same period. As catch figures were not available on a daily basis but only from monthly returns the Schnabel method could not be applied in its original form, but the formula has been used in conjunction with the monthly catch figures by using a moving group of 3 months' figures in a manner comparable to the use of moving averages to produce smooth trends. This adaptation of the method might be thought to magnify the possible errors resulting from departures from the assumptions of the ideal situation. However, as the tables reveal, the estimates from this method of computation do not in most cases differ in order of magnitude from those derived from the Petersen method.

TABLE 1

AVERAGE WEIGHT OF FISH BASED ON SAMPLING OF COMMERCIAL CATCH

Species	Weight (lb)
Sea mullet (*Mugil cephalus*)	0·66
Flat-tail mullet (*Liza argentea*)	0·50
Bream (*Mylio australis*)	1·00
Luderick (*Girella tricuspidata*)	0·66
Squire (*Chrysophrys auratus*)	0·50
Leatherjackets (*Meuschenia trachylepis* and *Monacanthus chinensis*)	0·25
Tarwhine (*Rhabdosargus sarba*)	0·50

The Petersen estimates were made only on the basis of the tags attached during the previous month. The Schnabel estimates considered the tags attached in the previous 3 months. The Schnabel estimations were extended beyond the time when tagging ceased, assuming for computation purposes that no losses of tags were occurring from causes other than fishing. The figures would be expected to increase as the effects of migration and recruitment were felt, and this is exemplified in Tables 2–8. In converting the catch figures, which are in terms of weight, to numbers the relationships in Table 1, based on a sampling of the Lake Macquarie commercial catch, were assumed to hold. Although 24 species of fish were tagged, only the eight listed in Table 1 were both tagged and recaptured in numbers sufficient to yield useful data. Mortality rates were estimated from the tagging data by the method of Ricker (1948). This method, involving returns over successive years, gave results patently too low, as might be expected from the three possible sources of error, emigration from the lake, a different rate of mortality amongst the tagged fish, and possibility of loss of tags. Mortality was therefore calculated by taking account of the change of rate of return of tags in the first 3 months after tagging, it being assumed for this purpose that inaccuracies due to immigration and emigration would be less in this time.

Table 2

POPULATION ESTIMATE OF SEA MULLET LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(*a*) Petersen Method			(*b*) Schnabel Method		
		Confidence Limits			Confidence Limits	
	Estimate	Lower Limit	Upper Limit	Estimate	Lower Limit	Upper Limit
1954						
May	2071	695	3420	1781	593	
June	3476	1614	5603	3395	1311	
July	2490	1156	3876	3137	1654	30170
August	4836	3077	6645	8101	4272	77895
September	954	322		829	469	3061
October	745	250		974	720	1508
November				582	270	
December	950	505	7917	632	333	6081
1955						
January	1865	630		2204	1162	21200
February	2046	943		2936	1373	17535
March	5943	1240		1493	787	14357
April	3194	2044	7301	2334	1485	5889
May	3897	1946	8977	2789	1981	4708
June	1740	520		3162	2414	5033
July	3501	1193		3761	2759	5926
August				4084	3063	6382
September				4417	3262	6842
October				4324	3274	6364
November				4674	3551	6833
December				4980	3795	7240
1956						
January				5496	4200	7948
February				5714	4402	8143
March				6028	4677	8467
April				5977	4717	8156
May				6132	4873	8269
June				6583	5231	8876
Mean May 1954–July 1955	2693			2540		

Although confidence limits have been estimated and recorded, these allow only for the statistical sources of error, which arise largely from the relative sizes of the sample and the real population. Scattergood (1954) and Delury (1954) among others have discussed the assumptions underlying the methods of estimations used. There is no need to discuss these in further detail here except to point out some features which are of particular importance.

TABLE 3

POPULATION ESTIMATE OF FLAT-TAIL MULLET LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(a) Petersen Method			(b) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1954						
May	203	122	590	275	118	621
June	258	120	548	290	120	554
July	3	1	86	35	23	72
August	15	9	43	21	15	34
September	131	77	436	94	70	143
October	103	55	863	84	48	134
November	107	37		26	19	44
December				20	16	26
1955						
January				24	20	32
February				30	24	40
March				30	24	39
April				35	28	45
Mean May–November	117			118		

The two assumptions necessary for the correct use of the mathematical transformations that are probably least likely to be true in the present situation are (1) that the marked fish were randomly mixed with the unmarked, and (2) that there was only an insignificant recruitment to the stocks during the course of the experiment.

Study of the movements of the fish (Thomson 1959*b*) suggests that except for the flat-tail mullet, *Liza argentea*, the fish tagged do not become randomly dispersed about the lake but that those inhabiting the portions of the lake north and south of the entrance do not pass from one half of the lake to the other. Consideration of the lake in two sections might solve this partially for some species, and in fact as the commercial fishery is permitted only in the southern part of the lake, except for a few months meshing in the open waters of the northern half of the lake (Thomson 1959*a*), the figures quoted here really refer to the population of the southern part of the lake only. Even within this portion, however, some species show little dispersion from the grounds on which they were tagged. This is particularly so with the yellow-fin leatherjacket and young squire which remain in one area for prolonged periods, moving only when the seasonal migration out of the lake takes place.

TABLE 4

POPULATION ESTIMATES OF BREAM LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(*a*) Petersen Method			(*b*) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1955						
January	24	11	157			
February	48	31	564	10	5	42
March	12	6	242	26	17	56
April	46	19		25	18	45
May	79	45	323	21	14	41
June	28	18	60	38	27	59
July	33	13		48	35	75
August				37	30	51
September				52	42	68
Mean January–July	38			28		

Owing to the lack of information on the catch per unit of effort over periods less than a month, it has been impossible to assess recruitment. This, however, almost certainly occurs at a greater rate in some periods of the year than others owing to the restricted spawning periods of most species. The effect of this and of immigration and migration has been overcome to some extent by using the tagging data only over periods of a month.

In brief it may be said that these sources of error, and others such as the possibility that not all tags recaptured were sent to the experimenters, depart from the conditions of the ideal situation, and produce estimates that are too great.

III. Results

(a) *Population Numbers*

(i) *Limitations of the Results.*—The estimates of numbers of the various species do not cover the same periods. Tables for each species are therefore presented separately. In some cases the tags returned were so few that the upper limit of error according to the formula became an unreal number which has not been entered in the Tables.

Table 5

POPULATION ESTIMATE OF LUDERICK LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(a) Petersen Method			(b) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1955						
February	161	123				
March	627	212				
April	169	57	920	124	51	
May	37	23	82	128	76	192
June	292	112	850	105	72	195
July				154	105	285
August				171	120	293
September				184	131	311
October				39	21	216
November	22	11	227	46	33	74
December				29	21	49
1956						
January				61	21	58
February				48	33	82
Mean April–June	130			101		

(ii) *Sea Mullet.*—The sea mullet is the most abundant commercial species in the lake and appeared most consistently in the monthly tagging records. The population estimates of sea mullet are set out in Table 2. A modification of procedure in the Schnabel method was introduced for the figures for September 1954 as it was obvious that the high figure for August would unduly increase the estimate for September in the light of the returns for the latter month and as indicated by the Petersen method. The September figure therefore takes into account only the data for September, and the October result considers the tagging data for two months instead of the usual three.

Table 6

POPULATION ESTIMATE OF SQUIRE LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(*a*) Petersen Method			(*b*) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1954						
September	2·4	1·6				
October	7·0	5·4	9·9			
November	5·0	4·3	6·5	3·7	3·0	4·9
December	1·0	0·5	8·9	1·8	1·4	2·6
1955						
January	1·4	0·9	3·2	1·9	1·5	2·7
February	1·1	1·0	1·3	5·0	3·9	6·7
March	4·9	3·5	8·5	2·6	2·3	4·1
April	1·4	0·9	6·0	2·8	2·4	3·2
May				2·7	2·4	3·1
June				2·6	2·3	2·9
July				2·4	2·2	2·7
August				3·0	2·7	3·2
Mean November–April	2·5			3·0		

Estimates from the two methods differ greatly only in August 1954 and March 1955. The estimates for September suggest a fall in population numbers in this month. The adult sea mullet normally migrate annually to sea on their spawning run but this generally occurs in late autumn. However, a drop in the catch figures in September also suggests that mullet were not available. Their unavailability may have been due to reasons other than going to sea, such as entering the creeks and lagoons around the lake or a large-scale movement into the northern (commercially unfished) part of the lake.

(iii) *Flat-Tail Mullet.*—This species does not attain such a large size as the sea mullet. It is relatively unimportant in the catch but the experimental hauls and the tag returns suggest that the population is larger than would appear from the catch figures. Flat-tail mullet were not so numerous as their relatives the sea mullet during the course of these investigations (Table 3).

TABLE 7

POPULATION ESTIMATE OF LEATHERJACKETS LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(a) Petersen Method			(b) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1954						
August	415	234	1831	39	22	164
September	53	39	863	133	87	212
October	126	67	1057	50	42	63
November	104	61	307	66	55	82
December	57	29	469	62	42	129
1955						
January				73	50	76
February	91	55	245	86	65	176
March	94	50	297	83	65	114
April	72	40	318	111	74	215
May	21	12	76	72	48	144
June				92	70	109
Mean Estimate August–May (less June)	115			78		

(iv) *Bream.*—The black bream is of some commercial importance, being fifth or sixth by weight in the catch. It is also a favoured angling fish. However, its numbers in the southern part of the lake do not seem very great (Table 4).

There are quite considerable discrepancies in the estimates derived by the two methods. This arises from the apparent variation of population number as derived by the Petersen method. The Schnabel method tends to smooth out such large variations, though even by this method the changes were considerable.

(v) *Luderick.*—The luderick is not of major importance in the commercial fishery but it is sought after by both commercial fishermen and anglers. As was the case with bream, there is considerable variation in the estimate between the methods, and considerable changes from month to month (Table 5).

(vi) *Squire.*—Squire are a young phase in the development of snapper. Small squire are abundant in the lake but most of them seem to leave the lake before reaching the legal minimum size. The population of legal-size squire is therefore small (Table 6) and the catch small also.

TABLE 8

POPULATION ESTIMATE OF TARWHINE LARGER THAN THE LEGAL MINIMUM LENGTH IN THE OPEN WATERS OF LAKE MACQUARIE

(thousands of fish)

Month	(*a*) Petersen Method			(*b*) Schnabel Method		
	Estimate	Confidence Limits		Estimate	Confidence Limits	
		Lower Limit	Upper Limit		Lower Limit	Upper Limit
1954						
November	3	2	5	8	6	12
December	12	8	21	23	19	29
1955						
January	4	3	10	17	12	27
February	10	7	24	15	12	21
March	7	3	15	12	10	16
April	31	10		11	9	14
May	8	6	12	12	10	15
June	12	8	29	11	9	13
July				11	10	13
August				12	10	14
September				11	9	12
Mean November–June	11			14		

(vii) *Leatherjackets.*—The two species, the yellow-fin leatherjacket and the centreboard, are lumped together in the catch statistics. Two other species, the rough leatherjacket, and the mosaic leatherjacket, are also included in the catch figures but very few of them are taken. It will be seen that there are considerable discrepancies between the two estimates (Table 7).

(viii) *Tarwhine.*—The tarwhine is a fish which inhabits the estuaries only in the young stages. The population numbers are fairly low (Table 8).

(*b*) *Mortality Rates*

The natural mortality rates and fishing mortality rates as calculated from long-term tag returns by the method of Ricker (1948) are given in part (*a*) of Table 9. These same indices calculated from the cumulative short-term (monthly) mortality rates estimated from the returns of tags during the month following tagging provide the estimates in part (*b*) of Table 9. The differences between the two natural mortality estimates could be interpreted as the losses due to migration from the lake which most species do undertake from time to time especially for spawning. But it would also include effects due to loss of tags from the fish bearing them, and the dilution of the exploitable population by recruitment or immigration of new fish. Even the short-term estimates may be low because of these effects, and they could also be low due to failure of the fish to become widely distributed among the exploitable population.

TABLE 9

ESTIMATES OF FISHING AND NATURAL MORTALITY FROM LONG-TERM TAG RETURNS AND REPETITIVE SHORT-TERM RETURNS

Species	(*a*) Long-Term		(*b*) Short-Term	
	Fishing Mortality	Natural Mortality	Fishing Mortality	Natural Mortality
Sea mullet	0·003	0·58	0·20	0·33
Flat-tail mullet	0·04	0·90	0·23	0·37
Bream	0·05	0·92	0·17	0·26
Luderick	0·05	0·90	0·09	0·49
Squire	0·02	0·98	0·23	0·33
Leatherjacket	0·03	0·93	0·19	0·41
Tarwhine	0·13	0·78	0·16	0·19

Both fishing mortality and natural mortality might be greater than the figures in Table 9(*b*) suggest, but the ratio of fishing mortality to natural mortality would not be altered. Because for sizes above the legal minimum natural mortality is greater than loss due to fishing, the natural mortality exceeds the fishing mortality by a considerable amount over the fishes' whole life.

The figures suggest that the most heavily exploited stock loses only 23 per cent. of its legal-sized individuals each year. But, as mentioned above, the real figure may be in excess of this.

IV. CONCLUSIONS

The freedom with which fish may enter and leave the lake makes it difficult to estimate mortality rates, both natural and fishing, and to calculate population numbers. The statistical sources of error could have been reduced by more intensive tagging. The results perhaps indicate that with limitations on the amount of tagging better results would have been attained by tagging only one species using the method of capture most successful with that particular species.

The original hope of estimating the total numbers of all commercial species failed because either some species could not be caught in sufficient numbers (e.g. morwong, flathead, and jewfish) or when caught the proportion surviving capture and tagging was very small (e.g. tailor and garfish).

Although, as explained, the true figure may be somewhat higher, the annual fishing mortality of from 16 to 23 per cent. is reasonable; and does not indicate any cause for alarm on the effect of fishing on the stocks. The natural mortality rate is certainly in excess of the fishing mortality rate, and the combined figure for most species is only a little over 50 per cent., with bream and tarwhine showing a lesser rate.

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SOME ASPECTS OF THE ECOLOGY OF LAKE MACQUARIE, N.S.W., WITH REGARD TO AN ALLEGED DEPLETION OF FISH

XII. SUMMARY REVIEW

By J. M. Thomson*

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Summary

The nature of the entrance channel determines the peculiar attributes of Lake Macquarie. The food of the fish appears to be derived ultimately from the benthic flora, including epiphytes, rather than from the plankton.

In terms of the commercial fish catch per man the lake is as productive as it ever has been; amateur angling is increasing in intensity and in midsummer rivals the effects of the commercial fishermen. The fall in catch of certain species during the decade 1946 to 1955 is attributed to the reduction of food consequent upon stratification of the lake waters after prolonged periods of heavy rain.

I. The Water

The special characteristics of Lake Macquarie are determined largely by the nature of the entrance channel connecting the lake with the sea. The channel is narrow and winding and in parts is very shallow, particularly at the inner end where a sand bar is encroaching on the lake. The channel has two important functions: firstly it damps the tidal amplitude and secondly it retards the discharge of freshwater to the sea (Spencer 1959).

For much of the year the lake is marine-dominated, for the catchment basins of the streams entering Lake Macquarie are very small and except during heavy rain the freshwater drainage into the lake is negligible. But during extended periods of heavy rain conditions of stratification are produced because the narrow channel permits the fresh water to escape only slowly and the shallow bar at the inner end of the channel holds the underlying saline water in the deep basin of the lake.

Tidal ventilation is poor. Even if all the water entering the lake during the course of a flood tide were retained until all the original "lake" was changed, it would take 100 tides to replace the lake's volume. This is important, for there is little contribution of nutrients, and particularly of nitrates, from the freshwater discharge into the lake, so that the nutrient supplies must be regenerated by a cycle within the lake or by replacement from the sea. As in most of the estuaries of southern New South Wales (Rochford 1951), the nutrient levels are fairly low, and similar to those of the adjacent sea. After prolonged dry spells the nitrate figures tend to zero though the phosphates do not reach exhaustion (C.S.I.R.O. Aust. 1956, 1957).

The chlorophyll content of the lake (Davis 1959) is similar to that of the open sea in the western north Atlantic (Riley 1939) or the Pacific off California (Graham

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1943) but lower than rich areas such as George's Bank in the north Atlantic (Riley 1941*b*) or Long Island Sound (Riley 1941*a*).

II. THE SUBSTRATE

A further consequence of the shallow sand bar is that neither tidal movement nor floods scour out the basin of the lake. The slow movement of water in the body of the lake permits even fine particles of silt to settle to the bottom as a soft ooze. It is significant that the bacterial flora of Lake Macquarie is more akin to that of terrestrial soils than to truly marine flora (Wood 1959*a*, Fig. 2). Pollution from both household and industrial sources is slight except in very localized areas. Like the soils from which they are derived these muds are deficient in minerals, particularly iron (Baas Becking 1959). On the other hand the phosphate content is twice as high as that for the average estuarine mud, indicating that the undisturbed fine bottom silt absorbs a considerable amount of this nutrient on settling.

To the eye a sample of mud from the bottom has a surface greasiness similar to that imparted by a diatom film. But microscopic examination shows that this is due to a layer of faecal pellets (MacIntyre 1959) and diatoms are in fact rare in the bottom ooze (Wood 1959*b*).

The shallower slope and weed zones display greater variety of niches, in fact they contain much less silt, are frequently sandy, and also have rocky and pebbly sections (MacIntyre 1959). The organic content of the substrate is much higher in these zones than in the muds from deeper water (Baas Becking 1959) and all the attached plants and sessile animals occur in these upper zones.

III. THE FOOD SUPPLIES

The phytoplankton content of the water is not great (Davis 1959; Wood 1959*b*) nor is the zooplankton population considerable (Kott 1955). Kott has suggested that "the zooplankton of Lake Macquarie is a particularly specialized, perhaps relic fauna, derived from the sea fairly recently". An alternative hypothesis is that except for the typically estuarine forms which may have self-perpetuating populations within the lake, the plankton is derived directly from the sea, but that survival and ability to reproduce differ in the lake environment so that the species that succeed within the lake are not necessarily identical with the dominants of the sea. It is considered significant that the stations nearest the entrance are richest in species and that certain species survive longest there (Kott 1955). The fact that certain benthic forms represented only by dead shells at the start of the investigations later appeared as young forms also suggests that the plankton from the coastal waters was successful in re-seeding the lake with these species.

Of the three benthic zones recognized the mud zone is the largest in area but produces the least biomass of invertebrate macrofauna (Table 1). Unfortunately estimates of the biomass of plant material and of microfauna are lacking. As the phytoplankton level is not very high it appears that the benthic plant material, sea-grasses, filamentous and blue-green algae, and diatoms provide the greater part of the basic food material of the lake.

The slope zone which is the smallest of the zones in area appears to contribute the greatest amount of invertebrate macrofauna to the food chain. The figures (Table 1) may be biased firstly because the possible error in the figures for the weed zone is large, and secondly because the figures from the slope zone are based on samples from one type of habitat only (MacIntyre 1959). Sampling difficulties prevented adequate estimation on the rocky slopes and areas typically covered by mussel clumps.

The mud zone is virtually a desert for all fish except the few that are able to utilize the tubiculous polychaet *Maldane sarsi* Malmgren and the ophiuroid *Amphioplus lobatus* Ljungman—the only abundant organisms. Only four species of the 103 fishes distinguished in Lake Macquarie have been found to feed on one or both of these species (Thomson 1959*b*). The weed and slope zones on the contrary support a wide variety of fishes of diverse habit. The proportions of the benthic zones of various types are more important than absolute areas.

TABLE 1

ESTIMATE OF THE BIOMASS OF INVERTEBRATE MACROFAUNA IN LAKE MACQUARIE

(with standard deviation of the estimate)

Zone	Area (sq. miles)	Biomass (kg)
Weed	9·84	2,395,000 ± 1,427,000
Slope	6·60	3,104,000 ± 206,000
Mud	25·34	695,000 ± 616,000

Only a small proportion of the fish species proved to be herbivorous. These, however, are most important in the fishing economy as two herbivores, the sea mullet and the luderick, together provided over 50 per cent. of the fish catch in Lake Macquarie (Thomson 1959*a*, Fig. 3), except in the years 1943–49, when the large catch of leatherjackets disrupted the normal proportions. However, there is reason to believe that these leatherjackets actually came from ocean waters outside the lake (Thomson 1959*a*), so probably even in that period the actual lake catch was dominated by these two herbivorous species.

The majority of the fish are carnivores and some, the piscivorous species, may be several steps removed from the basic food plants. Although data on the kinds of food preferred by the fish are available, no knowledge exists of the amount required daily for normal maintenance and growth nor of the rate of regeneration and growth of food materials. Consequently no estimate can be made of the fish-carrying capacity of Lake Macquarie.

IV. THE FISH

The commercial fish catch has been smaller over the last few decades than in the early days of the fishery (Thomson 1959*a*). But a large part of the lake has been closed to commercial fishing in later years and the number of fishermen is considerably smaller. In terms of the catch per man, which is a truer indication of the abundance of fish, the lake is as productive as ever. Also the lake is yielding an increasing quantity of fish to amateur anglers, whose catch cannot be estimated except on the basis of the tags returned compared with the number returned by commercial fishermen. It was possible to approach the professionals personally to solicit their cooperation in returning tags, whereas the amateur angler was contacted only through notices on boards, the press, and radio. It is therefore probable that the proportion of anglers cooperating was smaller than that of the professionals.

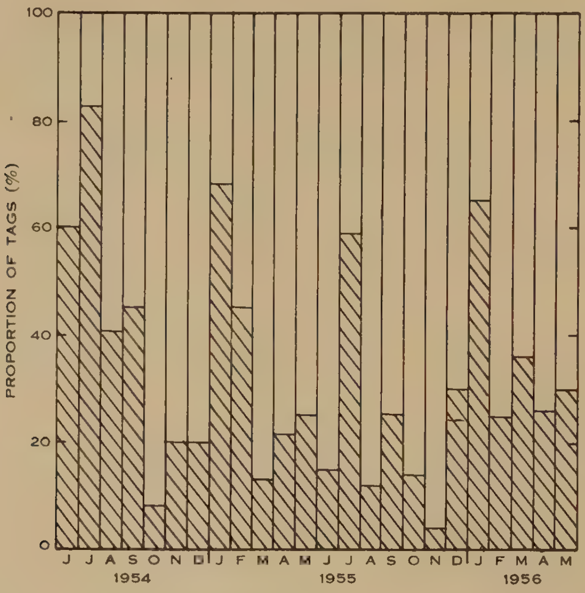

Fig. 1.—Proportion of tags returned by anglers (hatched) and professional net fishermen (clear) from Lake Macquarie, June 1954 to May 1956.

The proportion of the angling catch varied with the seasons and in the two years studied in detail, the angling returns in January, the main holiday month, increased to exceed the return from commercial fishermen (Fig. 1). The high proportion of returns by anglers in July of each year is not due to an increased angling catch but to a decrease in the proportion taken by the professional fishermen.

Besides being a source of commercial fish, Lake Macquarie is a nursery area for other species, particularly snapper. Few squire (young snapper) of legal size are taken (Thomson 1959*d*) but small specimens are easily caught in the lake. Their abundance in Lake Macquarie may be related to the large proportion of the mud zone in the lake, as the squire feed largely on *Maldane*, the polychaet which is the dominant of the mud zone. A much increased prawn catch could be made in the lake by permitting otter trawling, but this would be detrimental to the young squire.

V. THE STATUS OF THE FISHERY

Attention was drawn by Baas Becking, Thomson, and Wood (1959) to the fact that there existed allegations that the fish stocks were depleted. In fact (Thomson 1959*a*) it was shown that in the period 1945–47 a real drop in abundance of certain species had occurred, and that recovery of the stocks had been slow. It remains to consider the likely cause of this phenomenon.

TABLE 2

SEA MULLET CATCH, SIZE DISTRIBUTION DATA

Year	Lake Macquarie				New South Wales			
	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample
1941	31	24–37	3·6	169	28	20–50	12·2	26900
1945								
1946								
1947	29	22–37	4·2	429	28	21–52	9·6	29885
1948	28	23–40	3·9	812	28	23–40	7·2	8363
1949	28	24–38	1·1	455	29	21–49	6·5	3778
1950								
1951*								
1952	30	26–48	6·2	1879	30	24–52	9·6	39371
1953	30	25–41	2·4	2331	30	25–48	7·4	33529
1954	31	27–44	8·2	1761	30	24–52	11·8	35788
1955	30	26–49	15·7	3319	30	25–55	19·7	29495
1956	30	26–44	11·9	1736	30	25–53	19·7	29331
1957	30	27–50	13·4	2220	30	24–57	10·8	35348

* Legal minimum length of sea mullet raised in 1951.

(*a*) *The Hypothesis of Depletion*

Although the term depletion is frequently used simply as a synonym for a drop in catch, in fisheries science the term is understood to imply a drop in catch due to a specific cause, overfishing (Van Oosten 1949).

A drop in catch in terms of weight can result from one of two effects: (1) the same number of fish may be caught but the weight be less because the fish are caught at an average lower weight; or (2) there are fewer fish.

The majority of estuarine fishes are caught in the first year after reaching the legal minimum size, and market samples (Tables 2–4) reveal no significant changes in the size distribution of the three of the five species concerned for which there are adequate data. The smaller range of the Lake Macquarie fish is to be expected considering the relative size of the two samples and the range of habitats from which the total New South Wales sample is drawn. In general changes in the Lake

Macquarie sample have paralleled changes in the population as a whole and the few departures from this have not been consistent nor continuing in any trend.

There was no sudden increase in the number of men fishing prior to or during 1945–47 to provide an overwhelming pressure on the stocks. It is true that in 1940–41 and 1941–42 the intensity of fishing increased so that the catch per man in the latter year reached its highest recorded value and the total catch was at its heaviest since 1923. It may be thought that this heavy predation may have reduced the number of young that should have entered the fishery in 1945.

TABLE 3

LUDERICK CATCH, SIZE DISTRIBUTION DATA

Year	Lake Macquarie				New South Wales			
	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample
1941	25	22–31	0	76	24	19–43	10·8	2499
1945								
1946								
1947	25	24–33	1·6	61	25	21–41	9·1	1982
1948	23	20–38	3·2	1637	24	18–43	6·7	2934
1949	24	20–39	0·4	1086	24	18–44	4·4	11910
1950	24	20–37	5·1	857	24	18–42	4·4	17028
1951	25	21–39	0·2	1346	24	20–38	4·1	19333
1952	24	20–32	0	1220	24	16–35	3·3	17562
1953	24	22–37	4·4	508	24	19–41	6·7	10509
1954	27	22–37	6·5	879	26	21–49	10·9	10090
1955	24	22–37	5·7	424	28	20–42	5·5	10360
1956	25	21–37	9·5	220	26	20–44	10·7	12281
1957	25	22–33	0·5	236	24	22–43	7·2	11664

In theory overfishing could result in fewer fish by the reduction in spawning stock with consequently fewer young being produced. But exploited populations seem to be stable and in fact there are no unequivocal demonstrations that there is a direct relationship between the number of spawners and the number of consequent young surviving to fishable size (Beverton and Holt 1957, p. 44). This is due to the fact that in most species fecundity is high, and mortality rate is not uniform throughout life, nor is it necessarily independent of the density of stock.

Apart from the fact that it would be a remarkable coincidence for four species of diverse fecundity, feeding and breeding habits to reach the depletionary state simultaneously, this phenomenon could not be an isolated happening in Lake Macquarie, as there is constant interchange of fish between estuaries. This is more clearly proven for some species than others, but two of the species concerned, sea mullet and luderick, have provided direct evidence of their participation in such movements from the return of tags (Kesteven 1953; Thomson 1959*c*). There is no evidence of a coast-wide drop in the catch of these species at this period, according to the Annual Reports of the New South Wales Fisheries Department.

(*b*) *The Hypothesis of Catastrophe*

The hydrological evidence (Spencer 1959) showed that in 1955 and 1956 during autumn when heavy rains occurred over a prolonged period, there was marked stratification of the water. In the lower saline layer there was a marked reduction of oxygen. It is suggested that prolongation of the period of stratification would have reduced the oxygen level still more, as vital activities requiring oxygen would have continued.

TABLE 4

BLACK BREAM CATCH, SIZE DISTRIBUTION DATA

Year	Lake Macquarie				New South Wales			
	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample	Modal Length (cm)	Range (cm)	Percentage over 35 cm	No. in Sample
1941								
1945	23	16–31	0·3	291	22	17–41	1·5	6319
1946	26	19–29	0	57	22	17–42	3·4	6599
1947	23	17–32	0·4	172	22	17–42	5·2	9543
1948	22	18–36	3·1	823	22	17–39	3·6	13720
1949	23	19–34	0·2	469	22	17–41	3·9	6109
1950	21	18–34	2·0	1075	21	17–40	3·3	15202
1951	23	18–37	3·5	275	23	18–49	5·6	6093
1952	22	19–33	1·0	199	22	16–39	3·6	7998
1953	23	20–32	0·8	375	23	17–39	3·3	6821
1954	24	20–33	4·4	494	24	19–40	4·0	8655
1955	23	21–32	1·0	525	23	18–39	5·2	8077
1956	23	21–33	1·3	232	23	19–40	6·9	6437
1957	23	20–36	6·2	529	23	19–43	6·6	8336

Examination of the rainfall records shows that there were at least four monthly periods since 1940 when the rainfall was either of greater amount or of greater daily intensity than in 1954–56 when the investigation was carried out (Fig. 2). A series of dry years preceded the heavy rain of 1946. On some of these occasions the oxygen content of the water may have been reduced to a level lethal for at least some species.

The abundant recent mollusc remains are evidence that some such catastrophe may have occurred. It may be presumed that the catastrophe would have affected other organisms such as polychaet worms or algae which have no skeletal remains to leave as evidence. The disposition of the dead mollusc shells suggests that the oxygen-poor layer of water must have been high up on the slope in some places. The wind-induced circulation (Spencer 1959) would provide the means for this. It has been suggested too by Baas Becking (1959) that the lack of iron in the substrate would make the lake particularly liable to deoxygenation.

As a result of the loss of food organisms the fish-carrying capacity of the lake would be reduced. The first rainy period in 1946 was a severe one, the mean daily fall being greater than at any other period although the total monthly falls for June 1950 and August 1952 were greater. Three years after this, in 1949, when the young stocks of maturing fish would have been expected to enter the fishery for the first time, more heavy rains came, to be followed by heavy rainfalls in the succeeding years, except for 1953.

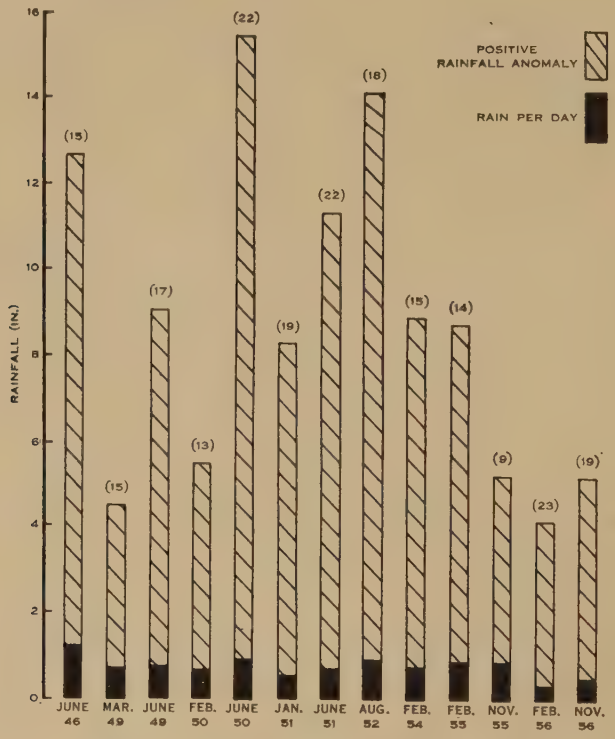

Fig. 2.—Monthly positive rainfall anomalies greater than 4 in. recorded 1943 to 1956 (hatched) with the intensity of fall as mean fall per days rain. The figures in parentheses above each column indicate the number of days in the month in which rain fell.

It is significant that when the survey started in 1954, many species of mollusc were represented only by dead shells and, in some cases, by very young live stages. As no resident populations of the majority existed in the lake re-seeding could occur only by transfer of planktonic larvae from the sea. This could be a slow process depending upon the conditions of plankton drift near the lake entrance. The continued rainy periods from 1949 to 1952 may have prevented the successful recolonization of the lake, if, as hypothesized, the rains of 1946 had had a catastrophic effect. The one benthic species whose size distribution made it obvious that it must have survived these periods is the mussel *Trichomya hirsuta* (Lamarck) which can survive long periods of adverse conditions (MacIntyre 1959).

Plants might be expected to recolonize more rapidly than animals and it may be significant that the two algal feeding fishes concerned have recovered more rapidly than the carnivores.

In the absence of contemporaneous observations on the state of the benthic fauna and flora prior to, during, and after the periods of heavy rainfall no proof of this hypothesis is possible. It is, however, in accord with the facts adduced during this study of the ecology of Lake Macquarie. If the hypothesis is correct it indicates that unless some means can be devised to drain the waters of the lake more rapidly, the situation will recur whenever very heavy rain falls over long periods.

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